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URBANA

REPORT OF INVESTIGATIONS—NO. 75

Contributions to Pennsylvanian Paleobotany

MAZOCARPON OEDIPTERNUM, SP. NOV.

AND

SIGILLARIAN RELATIONSHIPS

By

JAMES M. SCHOPF

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URBANA, ILLINOIS
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Topographic Mapping in Cooperation with the United States Geological Survey.

This Report is a Contribution of the Coal Division, Geological Resources Section.

August 1, 1941

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PREFACE

Applied research on coal has revealed the fact that there is a dearth of fundamental information regarding the nature of the original plant material from which the coal was derived. It is therefore necessary to carry forward a parallel program of fundamental studies whose results should give new concepts that will make applied research even more productive.

The present paper represents an important contribution to the knowledge of spores and to the relationship between certain types of spores and certain kinds of trees that contributed to the mass of vegetation from which the coal beds were derived.

Among the constituents of coal there are certain plant tissues that endure better than others the changes, severe compaction, and other solidification effects of the transformation of plant material into bituminous coal. Even in the compressed solid material of the coal in Illinois, such tissues or organs can be found so little altered from their original appearance that they can be readily identified. Also, because of their relatively great resistance to oxidation by chemical reagents, it is possible to isolate them completely from the rest of the coal so that they can be examined and photographed. The most interesting of these forms are the plant spores, which may make up a large percentage of the mass of a coal and hence definitely affect the property of such a coal, and which are also valuable as a record of the forms of vegetation that contributed to the coal bed. The present paper is concerned mainly with the investigation of certain parts of the kinds of plants of which the coal beds are composed.

The spores vary considerably in their outer form and appearance because of differences in shape and differences in the kind of ornamentation. Shape and ornamentation have been used by paleobotanists as a basis of elaborate and complicated form-classification of spores. This is largely because of the uncertainty as to the identity of the spores in terms of the parent tree.

For the purpose of relating spore varieties to definite plants, it is fortunate that Illinois coal beds have yielded several important deposits of fossilized peat in the form of coal-balls. These coal-balls are petrified masses of peat material which is preserved essentially in the condition in which it existed in the peat deposit before the overlying strata were deposited. Calcite was deposited in the open cell spaces and in all other

open spaces in the peat or in spaces filled only by liquids, thereby fixing the tissues in their relatively unconsolidated form. Such fossilized peat contains all the kinds of plant forms that compose the surrounding normal coal bed. Spores are not uncommon components of the coal-balls, but what is more important to the paleobotanist is the fact that spores are found associated with the organs from which they were produced and the cones containing such organs. Once certain cones and certain spores are definitely linked together, it becomes much easier to identify the spores in terms of the plants from which they were derived. Thus a step in the process of classifying spores in a natural way is accomplished.

Extended investigations of this kind will be necessary before a satisfactory understanding of the relationships of spores found in Illinois coals will be attained. Since it is only a matter of chance that cones containing spores will be contained in any coal-ball, advantage should be taken of the opportunity to study new varieties of cones whenever such discoveries are made in order that the classification of the spores may proceed as rapidly as possible.

All of this work should lead to a taxonomic classification of the plants which make up the coal beds—a classification which may ultimately play as important a part scientifically and industrially as the classification of our modern flora has played.

—Gilbert H. Cady,
Senior Geologist and Head of the Coal Division.

of Carboniferous plants that have sigillarian alliance.

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Contributions to Pennsylvanian Paleobotany

MAZOCARPON OEDIPTERNUM, SP. NOV.

AND

SIGILLARIAN RELATIONSHIPS

BY

JAMES M. SCHOPF

INTRODUCTION

THE PURPOSE of this paper is to describe a new species of plant which is illustrated by a remarkable series of cones from the Calhoun (Richland County) coal-ball horizon in Illinois.

Mazocarpon oedipternum, although scientifically interesting in itself, is significant chiefly because it helps to clarify the relationship between groups of Carboniferous plants that have sigillarian alliance.

The close relationship of *Mazocarpon* and *Sigillaria,* previously suggested by Benson (1918) and Hagéne (1926), receives additional support in the evidence presented in this report. *Sigillariostrobus* and *Mazocarpon* are shown to be closely allied, and one of the most important results of this study is recognition of the relationship of spores classified under the section *Aphanozonati* of *Triletes* and the sigillarian alliance.

The conclusion that the *Aphanozonati* represent a natural closely allied group of plants was reached in an earlier study (Schopf, 1938, b, pp. 23-24). At that time it was not known what particular group of lycopods was represented nor how trustworthy spore resemblances were for evaluating plant relationships. Spores of the sigillarians (the *Aphanozonati)* now appear to be identifiable throughout the Pennsylvanian system. By analogy, and in the absence of conflicting evidence, resemblances among other kinds of spores assume a greater importance since we have the present example to indicate that botanical affinity between species based on spores alone can be established with reasonable precision.

Recognition of the botanical affinity of the *Aphanozonati* greatly increases the usefulness of these spores in coal studies and in stratigraphic paleobotany. Well-preserved megaspores can generally be recovered even from thin coal beds, carbonaceous shales, and carbonaceous sandstone laminae which do not provide other identifiable fossils. The possibility of identifying spores in terms having definite botanical significance increases their usefulness in stratigraphic correlation and in plant population studies. In the latter capacity they may aid in explaining differences in constitution among the various types of coal.

Although the affinity of the aphanozonate megaspores is probably of greatest immediate interest, the related cones provide a good deal of additional paleobotanical information. Heretofore the anatomy of sigillarian fructifications, and particularly of the microsporangiate structures, has been inadequately known. Microsporangiate cones are now described from abundant material. Well-preserved female gametophytes can also be described more completely than was possible before. Thus considerable new information is available to illustrate the reproductive phases of a sigillarian life cycle.

The present paper by no means exhausts the possibilities of botanical study on the Calhoun collections of *Mazocarpon*. It seems desirable, however, to publish the data which are now available so that they may be of use. A complete study of this excellent material will require much more time.

ACKNOWLEDGMENTS

The author wishes to express his appreciation to Dr. G. H. Cady for encouragement during the progress of this work, and particularly for his careful reading of the manuscript and his constructive comments. Mr. Revilo Oliver of the University of Illinois Classics Department has aided in the selection of the new scientific names. Professor L. M. Cline of Iowa State College, Ames, has kindly provided correlations for several coal-ball occurrences in Iowa. The assistance of Professor H. R. Wanless and Dr. J. M. Weller in stratigraphic interpretation and the cooperation of other members of the Survey staff is gratefully acknowledged. Many of the sections used in this study of *Mazocarpon* have been prepared by Mr. E. Allen Platt.

AGE RELATIONS OF COAL-BALL PETRIFACTIONS WITH REFERENCE TO THE GENUS *MAZOCARPON*

The occurrence of *Mazocarpon* in the upper McLeansboro Calhoun coal-ball horizon was first reported by Graham in 1935. A published list (Fisher-Noé, 1939) of coal-ball plants from the Calhoun (Richland County) locality refers to this form as *Mazocarpon shorense* Benson, although *M. shorense* had been reported previously only from much older lower Westphalian strata in western Europe, and Graham's mention of *M. shorense* in this connection was only comparative. It now appears that the Calhoun *Mazocarpon,* i. e., *M. oedipternum,* is distinct from *Mazocarpon shorense.* The improbability of the species being the same is evident from consideration of the difference in age between well known European and American coal-ball horizons.

The horizon at which any fossil specimen is found is important in considerations of its relationship and phylogeny. Hence it is essential that the geological age relations be critically considered before conclusions are drawn as to the biological relationship of species of *Mazocarpon* and the species of other genera closely related to it.

Correlation of Carboniferous beds in America and Europe, or even between different coal fields in either continent, still offers many problems, but a tentative correlation may be arrived at which enables us to place the Calhoun material in its approximate position in the time sequence. This is summarized on the chart given in text figure 1. Further information is given in the many papers published in the Proceedings of the 1927 and 1935 Heerlen Congresses on Carboniferous Stratigraphy.[1] Miss Dix's (1937) correlation of English Upper Carboniferous with the standard Westphalian section has been helpful. Hirmer (1940) has recently summarized in detail the stratigraphic extent of Upper Carboniferous floras in northwestern continental Europe, and Jongmans (1940) has given a useful summary of the British Coal Measures stratigraphy. Wanless' (1939) recent correlation of the Appalachian and Eastern Interior basins is the most satisfactory treatment available dealing with this difficult subject. More recently, stratigraphic classification of the Pennsylvanian system in Illinois has been revised (Weller, 1941). The Caseyville, Tradewater,[2] Carbondale, and McLeansboro beds are now recognized as groups instead of forma-

[1]Exact titles cited under "Heerlen" in the list of references, pp. 38-40 of this report.

[2]Use of the term "Pottsville" as applied to beds of Caseyville and Tradewater age has been discontinued by the Illinois Geological Survey. The Pottsville beds are generally accepted as equivalent to the Pocahontas, New River, Kanawha succession in the Appalachian region.

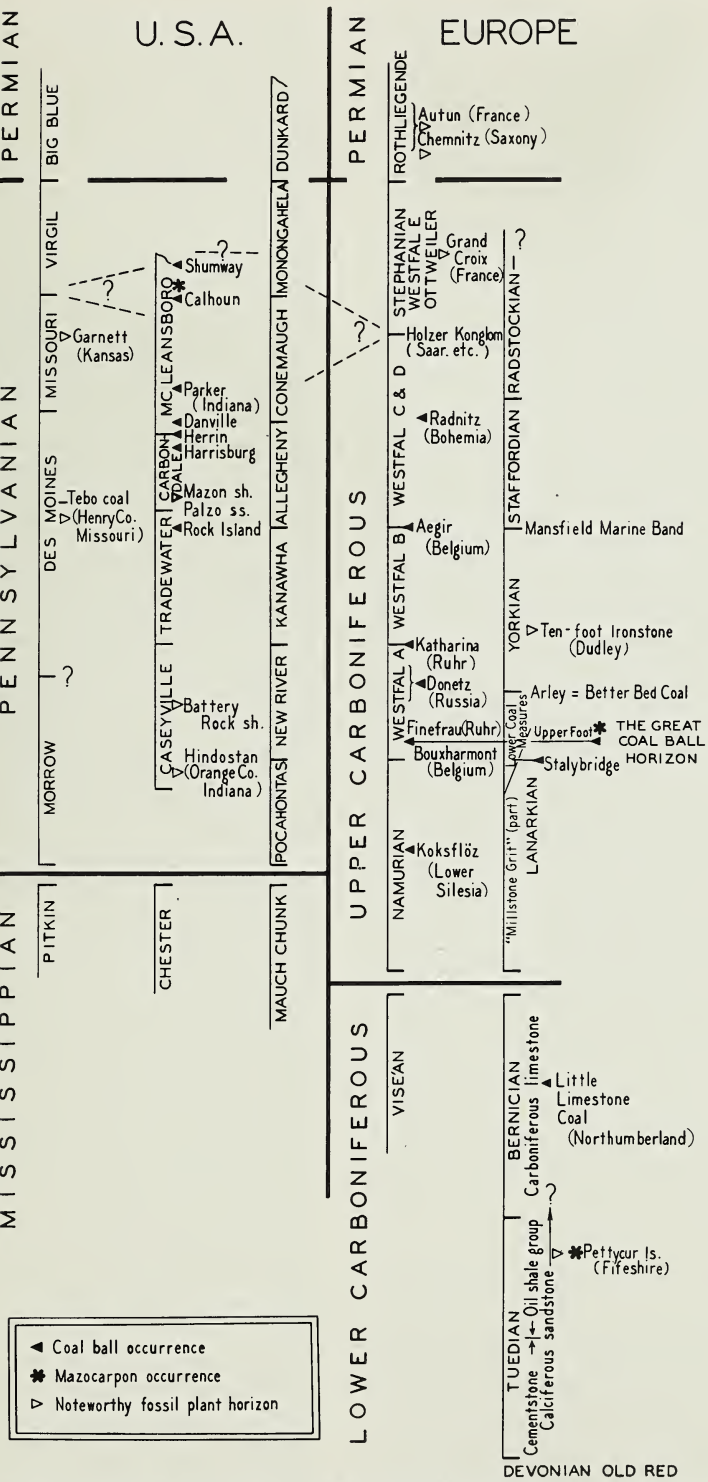


FIG. 1—Chart showing correlation of Carboniferous beds in America and Europe.

tions by the Illinois Geological Survey. Details of the mid-continent section have been discussed by Moore (1936).

Most trustworthy intercontinental correlations apparently can be made between the middle Pottsville New River beds and the Westphalian A. For example, Bertrand (1933, 1935), Moore (1937, p. 671), and D. White (posthumous unpublished manuscript recently completed for publication by Charles B. Read) have all suggested that the Namurian-Westphalian boundary is at least approximately correlative with the Pocahontas-New River boundary in the American Pottsville. The Carboniferous-Permian boundary seems fairly well established in some areas but is still controversial in others. Thus the relative age of the three species of *Mazocarpon* that are now known can be established approximately, and this is the first step in understanding the phylogeny and in adding to the stratigraphic usefulness of this group of plants.

Mazocarpon is generally definable only on the basis of petrifactions, and these are most commonly found in Carboniferous rocks as fossils in coal-balls. Further investigation of coal-ball fossils will doubtless supplement the somewhat scant information now available as to the occurrence of *Mazocarpon* and will also provide other fossils of geological and botanical importance. Because of this, and the fact that the relative stratigraphic positions of various coal-ball horizons have commonly been disregarded, most of the significant coal-ball horizons of America and Europe have also been indicated on the chart (fig. 1) in their approximate relative positions. A few other horizons, significant in correlation or as a source of important plant fossils, also are indicated.

ILLINOIS COAL-BALL HORIZONS

Seven coal-ball horizons are now recognized in the Illinois basin, and others will probably be discovered. Two, the Shumway and the Parker, are here reported for the first time.

Coal-balls from the Shumway coal, at the top of the Illinois section, contain chiefly fern material. They differ from most other coal-balls in that they are silicified, but since they are entirely included within a 6- to 10-inch coal bed and show the characteristic type of plant tissue preservation there seems to be no reason why they should not be called "coal-balls". The occurrence is unusual because silicified plant material is not ordinarily found in Illinois coal beds. David White (1925, p. 10) attributes the "segregative precipitation of colloidal silica" to rapid invasions of saline or brackish water at the time of, or very soon after, deposition of the plant material. Unfortunately, he did not cite instances which he undoubtedly had in mind, and we have no way of knowing whether the Illinois silicified coal-balls correspond exactly with his interpretation or not.

The next lower coal-ball occurrence is the Calhoun (Richland County) coal horizon from which the new species described in this paper, *Mazocarpon oedipternum*, was obtained. The Calhoun horizon is in the upper part of the McLeansboro group of Illinois. Recent studies have indicated that the Calhoun horizon is stratigraphically higher than it was previously considered by Newton and Weller (1937). Its relative position is somewhat uncertain although it is known to be considerably higher than the LaSalle limestone.[3] The limestone that overlies the Calhoun coal bed, and is continuous in a few places with the pockets of coal-ball concretions in the coal bed itself, has been called the Calhoun limestone by Grogan and Lamar (1940, p. 42). About 800 feet below it is the Herrin (No. 6) coal which marks the top of the Carbondale group in Illinois. Feliciano (1924, p. 232) has listed coal-balls from the Calhoun locality as if they were from the Herrin (No. 6) coal, but the Herrin coal is not mined and does not crop out in this part of the State. Miss Reed (1939, pp. 770-771) has stated that the Calhoun coal-balls "are of the same geologic age as those from Harrisburg," but the Harrisburg coal-balls are from the second coal below the Herrin (No. 6) coal, and are thus from the Carbondale group.

[3]Weller, J. M., personal communication.

Coal-balls were obtained at about the horizon of the Parker coal in Posey County, Indiana, in 1938. This occurrence was first discovered by John Lester, formerly of the Stratigraphy and Paleontology Division of the Illinois Geological Survey. The position of this coal in the stratigraphic sequence has been placed by J. M. Weller a short distance above the horizon of the Lonsdale limestone. Collections have been made but are still unstudied, although characteristic fossils of *Psaronius* and *Mycloxylon* have been observed.

Coal-balls from the Danville (No. 7) coal (very near the base of the McLeansboro group) have been reported by Feliciano (1924) and others. Coal-balls reported from near New Castle, Texas, cannot be definitely correlated with the Danville (No. 7) coal, as the chart published by Feliciano suggests, and this record at present seems inconclusive because no plant material has yet been reported.

Numerous coal-balls have been obtained from the Herrin (No. 6) coal at the top of the Carbondale group, first reported at Nashville, Illinois, by Cady (1936). Recently other occurrences have also been discovered in the Herrin coal. The Harrisburg (No. 5) coal is the second coal bed encountered below the Herrin coal in the vicinity of Harrisburg. The first American coal-ball to be recognized as such was obtained from the Harrisburg coal by Dr. G. H. Cady and transmitted to Professor A. C. Noé who later collected more of them. Several studies of coal-ball plants from this collection have been published by J. H. Hoskins, H. V. Krick, and F. D. Reed.

The lowest horizon in this basin to have provided coal-balls is the Rock Island (No. 1) coal in the upper part of the Tradewater group. At least five thin but generally persistent coal beds occur above it and below the base of the Carbondale group.[4] The Silverwood (Silver Island) coal-ball occurrence reported by Feliciano (Fountain County, Indiana) is in the Minshall coal which is equivalent to the Rock Island coal according to Wanless (1939). Coal-balls have been recorded from central Iowa west of Des Moines by Darrah (1939). The coal is reached by shaft mines, and its position is less definitely established than that of the other horizons mentioned, but according to Dr. L. M. Cline the coal is probably the same as Lugn's (1927) Lucas County "Lower Coal", which may correspond in age to the Rock Island bed of Illinois. Darrah mentions that *Mazocarpon* occurs in these coal-balls but the results of his study are not yet available. Coal-balls considered to be from the same horizon have been obtained near Indianola, Iowa, by Hoskins and Cross (1941). Other Iowa coal-ball material is being studied by L. R. Wilson and his students at Coe College.

Feliciano also listed coal-balls collected by Noé from Bloomfield, Davis County, Iowa. The only coal-balls known in this vicinity are from the Lower Seahorne coal, according to recent studies by Cline. This coal is above the Rock Island horizon, in the upper part of the Tradewater group.

EUROPEAN COAL-BALL HORIZONS

Histologic preservations of plant debris of lower Permian age has been reported from western Europe in many studies. Similar material of Stephanian age in central France has also been the subject of much investigation. Most of these petrifactions are silicified. Although the plants are comparable in preservation to those from coal-balls, they apparently have no relationship to beds of coal, and consequently the petrifactions must have been formed differently. They are mentioned because they seem to provide the most abundant comparable paleobotanical material that is younger than that in Illinois coal-balls, and some of the plants found here may have an ancestral relationship to some found in Stephanian and lower Permian deposits.

In 1845 Corda (1867) described in the "Protogaea" a few plants from the coal mines near Radnitz in central Bohemia which were histologically pre-

[4]The Palzo sandstone member is now considered to represent the basal bed of the Carbondale group (Cady 1941). Wanless (1939) used the Sebree=Isabel? sandstone as a boundary, but the precise equivalence of those beds is in question and the Isabel, at least, may lie somewhat higher than the Palzo.

served and apparently similar to those in coal-balls. Kubart (1911) later reexamined some of Corda's original material but was unable to obtain any new specimens or ascertain the original source. Nemejc (1937, p. 687) has characterized the floras of Carboniferous strata of the region and concludes that they range in age from the transition at the top of Westphalian B into the Permian but that the lower Stephanian is not present. Presumably Corda's coal-balls came from somewhere in this sequence, probably (judging from the fossils) from the upper Westphalian. Little is known about fossil plants in coal-balls reported by LeClerq (1925) from the Petit Buisson coal (Aegir) horizon in Belgium. Fossil plants in coal-balls from the Katharina coal in Limberg in Holland and the Aachen district in Germany are well known, chiefly through recent investigations by Hirmer. Lists of species present and other references are included in his papers cited for 1928 and 1938. This bed is generally accepted by European geologists as the boundary between Westphalian A and Westphalian B. Coal-balls are reported by Zalessky (1910) from the Donetz basin in Russia, the most important of which seem to be slightly older than the Katharina horizon and therefore in the Westphalian A, but no very thorough studies are known to have been made.

The most important of all European coal-ball horizons occurs in the lower part of the Westphalian A. One persistent coal bed, which may be traced from Westphalia into Belgium and is recognized in central England by the presence of an overlying characteristic "marine band," has provided the majority of species of coal-ball plants now known. Among them is *Mazocarpon shorense* Benson. Important work was done on coal-ball fossils from this bed by English botanists particularly. In England the coal seam is known as the "Halifax" or "Hard Bed" coal, as the "Bullion", "Mountain mine" etc. In Lancashire, where it splits into two beds, the upper bed is often called the "Upper Foot Seam" and the lower one the "Ganister". In Belgium the correlative seam is the "Bouxharmont" and in Limberg (Holland) and in the Ruhr it is the "Finefrau-Nebenbank". Because of its importance as a source of coal-ball plant fossils this horizon may be termed the Great Coal-ball horizon. It seems that for many years coal-ball fossils found in this country and elsewhere will require comparison with forms previously described from this Great Coal-ball horizon, as it is the only one whose flora is adequately known.

Stopes and Watson (1909) showed that the seam which contains coal-balls long known from localities near Stalybridge and Hough Hill was lower than the Ganister (Great Coal-ball) horizon. Miss Benson also obtained *Mazocarpon shorense* from these localities. Coal-balls were also reported by Stopes and Watson from above the level of the Great Coal-ball horizon in central England in the "Great Harwood" seam, and in the "Arley mine" coal at the top of the "Lower Coal Measures" (Upper part of the Lanarkians). Floras from these coal-balls have not been described to the author's knowledge.

Kubart (1908, 1914) described a few very interesting pteridospermic species from coal-balls in the Koksflöz in Lower Silesia whose occurrence had been described by Stur in 1885. The stratigraphic position is apparently well defined, as this seam is the highest in the Rand group, with marine beds above it, and the Pochhammerflöz, lowest coal of the Sattelflöz group, is superjacent at a short interval. The boundary between the Rand and the Sattelflöz groups recently has been more precisely correlated with standard sections by Czarnocki, Bode, and others (cf. C. R. 2nd Heerlen Congress).

Coal-ball plants were reported by Absalom in 1929 from the Little Limestone coal of the Lower Limestone group in the Carboniferous Limestone series of Northumberland. Thus far the occurrence is chiefly significant because a few species seemed to be present which had previously been identified from the Upper Carboniferous Great Coal-ball horizon. If they are correctly identified (Crookall, 1939, does not accept the determinations w i t h o u t reservation) these species transgress the important

"floral break" first recognized by Kidston in the English Carboniferous.

One other important source of fossil plant material comparable to that in coal-balls is in the Calciferous Sandstone series of southern Scotland. The Pettycur limestone on the Firth of Forth in Fifeshire is most notable, particularly since a third species of *Mazocarpon, M. pettycurense,* comes from this locality. The age equivalence of this limestone (a brecciated travertine according to Gordon, 1909) is apparently not precisely definable because it occurs in a thick sequence of pyroclastic rocks and beds that lack suitable zonal fossils. Allen (1924) has given a rather detailed section taken around the coast on the north shore of the Firth of Forth which must include the Pettycur limestone, although the bed is not identified as such. Apparently its position is somewhere within the upper Oil Shale group. Generally speaking, the Calciferous Sandstone may correlate with beds of Lower and in part Middle Mississippian age in America, which include the Pocono-Price of continental facies in the eastern Appalachians and marine beds in the Illinois basin.

DISCUSSION

The Pennsylvanian of Illinois has been correlated with that of the Appalachian trough by Wanless (1939) and others. As mentioned previously there is some agreement of opinion concerning correlation of the New River beds (middle Pottsville) with the Westphalian A. Thus it is possible to arrive at an estimate of the time interval separating the Calhoun horizon (containing *Mazocarpon oedipternum*) and the Great Coal-ball horizon from which *Mazocarpon shorense* was described. Since the latter horizon is not far above the base of the Westphalian A, its equivalent would be in the lower part of the New River group in West Virginia. According to Wanless (1939; also oral communication) this would correspond, in Illinois, to some horizon probably below the Battery Rock coal of the Illinois Caseyville group.

There is questions as to the proper correlation of the upper part of the McLeansboro group in both the Appalachian and mid-Continent areas. Tentative correlations by Moore (1936, pp. 71, 144) suggest that the Missouri-Virgil boundary is about equivalent to the age of uppermost McLeansboro beds of Illinois and is somewhere near the Conemaugh-Monongahela boundary of the Appalachian trough. Weller (personal communication) has recently considered that the McLeansboro beds may range somewhat higher than this.

Thus the disparity between time of deposition of the two coal-ball horizons in question is equal to the greater part of the Illinois Pennsylvanian section, including equivalents of much of Conemaugh, all of the Allegheny and Kanawha, and a considerable part of the New River time intervals. The tendency in the past has been to place the Illinois McLeansboro beds higher in relation to the European section than is indicated on the chart (fig. 1), therefore it appears that the present estimate of the time interval is a conservative one, and the age discrepancy between these two coal-ball horizons may actually be greater. *Mazocarpon pettycurense* from the Pettycur limestone is, of course, much older than either of the Upper Carboniferous species.

The genus *Mazocarpon* appears therefor to have a proved range extending fairly well through the Carboniferous. The Calhoun occurrence is by far the youngest. The infrequency of reports of *Mazocarpon* probably has been due to lack of attention given to material from which it might be identified. That this is the case is supported by evidence derived from other closely related groups of plants, discussed later, which are well known from intervening horizons. The continuity of *Mazocarpon* throughout the Upper Carboniferous is important in that it shows more decisively than was possible heretofore that the sigillarians are a discrete group of plants, distinct from other groups of arboreous lycopods, such as *Lepidodendron, Lepidophloios* etc. that are also present in the same series of beds. As such groups become better defined the possibility of applying methods of phylogenetic paleontology becomes increasingly more practical.

DESCRIPTION OF NEW MATERIAL

Mazocarpon Benson, ex Scott, 1909

1909—Scott, D. H., Studies in Fossil Botany, 2nd ed., pp. 187-8, fig. 78.

1918—Benson, M., Ann. Bot., vol. 32, pp. 569-589, pls. XVII, XVIII.

Mazocarpon is a group of plants represented typically by cones that show certain histologic and morphologic features. Taxonomically the genus is satisfactory since the name is free from ambiguity. Similar cones preserved as impressions or compressions usually are best referred to *Sigillariostrobus* since ordinarily such preservation does not permit the identification of *Mazocarpon*. *Mazocarpon* and *Sigillariostrobus* are not synonymous because their respective diagnostic features are different, but from a biological standpoint the two genera overlap to an as yet undefinable degree. *Sigillariostrobus* is more broadly defined than *Mazocarpon,* and a more diverse array of species is included in it. It is by no means certain that all species assigned to *Sigillariostrobus* are closely related. *Mazocarpon,* on the other hand, is unquestionably a homogeneous group. It is possible that forms previously assigned to *Sigillariostrobus* may eventually be referred correctly to *Mazocarpon*. *Mazocarpon,* having the more precise systematic meaning, is preferable to *Sigillariostrobus* if a situation should arise in which choice is permissible between them.

Scott originally published the name *Mazocarpon* and credited it to Miss Benson, although her more complete account of the genus did not appear for several years. Scott stated that "*Mazocarpon* [is] distinguished by the fact that the megaspores in the sporangium are embedded in a massive parenchymatous tissue". This single characteristic will serve to distinguish the genus, since a comparable development of intrasporangial tissue is not known to be present in any other group. Miss Benson's discussion provides nearly all the detailed information that was known of *Mazocarpon* prior to discovery of the present material. Both Scott (1921) and Hirmer (1927) have summarized the information Miss Benson provided and offer a few additional comments and photographs of megasporangia. Both LeClercq (1925) and Koopmans (1928) have described *Mazocarpon* from the Great Coal-ball horizon, in Belgium and Holland respectively.

Mazocarpon shorense, described by Miss Benson in 1918 is the genotype.

Mazocarpon oedipternum sp. nov.

Plates 1-6

Heterosporous lycopsid plants, possessed of unisexual cones. Cones of medium size, about 12 mm. in diameter and 10 cm. or more in length; pedunculate; characteristically deciduous in their entirety. Sporophylls apparently either verticillate, five or six to a whorl, arranged in alternating series, or attached in a low spiral. Sporophylls fairly persistent on the cone axis. Axis 2-3 mm. in diameter, consisting of a narrow sclerotic shell less than 200 μ thick, equivalent to the outer cortex. The vascular system is centrally placed and consists of stele and sporophyll traces. Only occasional bits of delicate internal cortical tissues are preserved. The stele is somewhat variable in diameter and in structure; it varies from ⅓-½ mm. in diameter and generally appears medullated with a few scattered central tracheids enclosed by prosenchymatous "pith" cells; sometimes the stele has little medullary tissue and appears as a solid vascular strand. Traces come off from it at a long slant and appear to enter the fourth whorl of sporophylls above their point of origin. In their horizontal course through the sporophyll the trace lies close to the adaxial side of the pedicel; distal to the sporangium there is a well-defined dorsal loop. Within the pedicel and lamina, tracheids of the trace are chiefly scalariform; in the axis, spiral and annular elements make up much of the sporophyll trace.

The mega- and micro-sporangiate cones and sporophylls are similar except for their sporangia. The pedicel is attached at right angles to the axis and has broad thin laminal extensions on either side. The bulbous dorsal ap-

pendage or "heel", strengthened with thick sub-dermal sclerenchyma, is a noteworthy characteristic of this species. The specific name *"oedipternum"*, i. e., swollen heel, refers to this feature. The lamina proper is exceptionally short (about 3 mm.), broad, and turned sharply upward forming about an 80° angle with the pedicel. A reconstruction of a megasporangiate sporophyll of this species is shown in text figure 2.

The megasporangium provides the significant characteristics identifying the genus and consequently the holotype of the new species is chosen from the megasporangiate cone material. There can be no doubt that the associated microsporangiate and megasporangiate cones belong to the same species. However, no organic connection exists between the different cones, and they are inherently different. There is no basis for comparison of certain specific details (chiefly spores and sporangia) of the megasporangiate and microsporangiate cones. Thus, since objective proof of identity is lacking to this degree, a minor taxonomic distinction is adopted and cones of the different sexes are referred to separate forms within the species.

Forma MEGALOPHORUM, forma nov.

Pl. 1, figs. 1-4; pl. 2, figs. 1-5; pl. 3, figs. 1-9; pl. 4, figs. 1-5; pl. 5, figs. 2, 6.

Cones as previously described, bearing megasporangia. Sporangia tapering, 3½-4 mm. broad adjacent to the cone axis; up to 5¾ mm. broad near the distal end. Sporangia are about 5 mm. long and average about 2.7 mm. high. The greater distal breadth is chiefly due to the occurrence of keel-like projections of tissue low on both sides of the megasporangia giving them a somewhat triangular shape in cross-section. These lateral keels flare distally, then turn sharply upward and converge at the upper distal tip of the sporangium to produce a typical up-pointed "toe" effect, as seen in radial section. Sporangia are covered with the characteristic prismatic or palisade layer of cells as in *Lepidostrobus*. The prismatic cell layer varies in thickness, being considerably thinner in two or three areas on top of the sporangia and below on both sides close to the pedicel attachment. No other mechanism of dehiscence is provided. The sporangial interior is filled by parenchymatous tissue which surrounds the eight megaspores on all sides. Megaspores are large, approximating 2 mm. in diameter, radially symmetrical, varying in form from plano-convex to strongly concavo-convex. Spores adorned only by a cellular "ramentum" borrowed from the intrasporangial tissue; spinous or other appendages absent. Gametophytes are present within some of the megaspores. The sporangia in these instances are more or less disorganized and broken. A single short-necked pyriform archegonium is formed directly below the spore apex; the venter is about 250 μ in diameter.

The holotype of *Mazocarpon oedipternum* and of forma *megalophorum* is that illustrated in plate 1, figures 1-4; plate 2, figures 2, etc. from coal-ball 136, of the Illinois Geological Survey collections in Urbana.

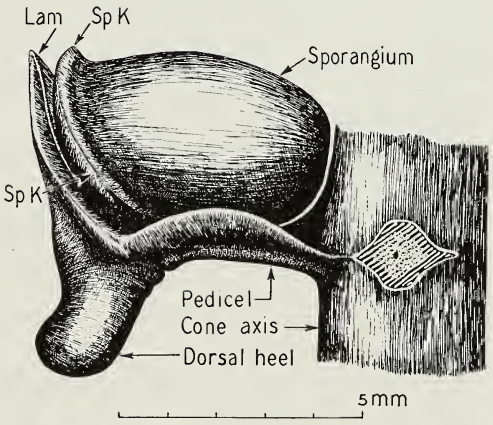


FIG. 2.—Reconstruction of sporophyll of *Mazocarpon oedipternum* forma *megalophorum*. SpK, sporangial keel; Lam, lamina.

Forma MICROPHORUM, forma nov.

Pl. 4, figs. 6-8; pl. 5, figs. 1, 3-5.

Cones, as previously described for this species, bearing microsporangia. Sporangia less inflated than in forma *megalophorum* due chiefly to absence of

persistent internal tissue and lack of lateral sporangial keels. Microsporangia about 2-2.8 mm. wide, about 4 mm. long and 2.5 mm. high. No intra-sporangial tissue is present in the mature microsporangium such as that present in the megasporangium; the prismatic wall layer is less rigid and more or less casual distortions often occur. In dehiscence a fracture occurs about halfway up on either side of the sporangium and extends over the top at the distal end. This line of fracture is equivalent in position to the slight concavity above the lateral keels of the megasporangia. Usually, the microsporangium is also broken from the pedicel; sometimes this causes another split at the bottom of the sporangium, and sometimes the spoon-like lower half of the microsporangium remains unbroken. The only trace of sterile tissue within the mature sporangium is a thin, somewhat variable, but often "T" shaped process attached radially part way along the pedicel. Immature microsporangia at the cone tip show that this is derived from the collapsed tissue of the subarchesporial pad. Spores are about 60 μ in diameter, slightly triangular, trilete, with rays extending to the equator. Exospore covered with numerous low papillae; endospore smooth and thin. At the point of each of the three pyramic segments of the endospore is a characteristic apical prominence. No endosporal male gametophyte has been observed.

Co-types of forma *microphorum* are the two cones illustrated in plate 5, figures 1 and 3 from coal-ball 124 in the Illinois Geological Survey collections.

MORPHOLOGIC FEATURES

Plates 1 and 2 illustrate the general features of forma *megalophorum*. Figures 1 and 2 of plate 1, and figure 2 of plate 2 represent parts of approximately radial sections of a fine cone. The three complete sporangia *a, b, c,* shown at the left in figure 1, plate 1, vary considerably. The upper sporangium *a* is cut radially but slightly to one side of the center so that the sporangial attachment to the pedicel is missed. Four megaspores are shown in characteristic arrangement. The lower sporangium *b* is also cut radially but on the other side of its center and shows little regularity of sporangial contents. The dark bodies shown are more or less distorted megaspores lacking their usual regularity of position. If eight megaspores are present it seems that some of them were abortive. Although this sporangium *(b)* has not attained normal development, the sporangium below it *(c)* apparently has grown larger to compensate for this, becoming almost spherical. The six spores shown in sporangium *c* are also displaced from their usual arrangement, but the increase in the size of the sporangium is accompanied by an increase in the amount of intra-sporangial tissue rather than by the development of more spores. The maximum number of megaspores was probably eight and these probably developed ordinarily from only two original tetrads. The manner in which the individual spores separated from the tetrad and came to be enclosed in tissue is still an unsolved problem, but may be due to anomalous growth of the subarchesporial pad. Hirmer's suggestion (1927, p. 284) that the eight megaspores developed from eight tetrads with three spores of each tetrad totally abortive, is unsupported by any positive evidence and makes the well developed trilete (haptotypic) structure of each mature spore very difficult to explain.

A normal sporophyll is shown in plate 1, figure 2 (N Sp) cut in almost perfect median section. Its sporangium, however, is separated from the pedicel and apparently was held in place only by the short upturned lamina. From this and similar examples, it is evident that as the cone broke up, the sporangia tended to separate from the pedicels. In *Mazocarpon shorense,* the entire sporophyll was shed as a unit, so that the separation of individual sporangia in *M. oedipternum,* rather than complete sporophylls, may also be taken as a specific distinguishing character. The dorsal loop of the sporophyll trace within the bulbous heel is plainly shown. The trace passes out of the section proximally so that it is not shown entering the axis. However, the proximal portion of a trace is shown by the second sporo-

phyll above, the lower part of which appears at the top of the figure.

The slender vertical stele (which is medullated in this cone) is shown in figures 1 and 2 cut on a long slant in the cone axis. Numerous outgoing sporophyll traces can be seen as thin discontinuous lines mounting at a steep angle in the inner cortical region which is otherwise nearly devoid of tissue.

Figures 3 and 4, plate 1, are tangential sections of the cone. Figure 3 is from a plane quite near the cone axis. The sporophyll arrangement here suggests a low spiral phyllotaxy, but this appearance may be due to a slight mechanical flexure. It is not proved that the sporophyll arrangement in this group of plants is inflexible; other specimens seem more conclusively in favor of a verticillate arrangement. The section in figure 4 is taken across the sporophylls just proximal to the great dorsal expansion of the heel. Each of the three sporangia shown has separated from its pedicel, in the manner also shown in figure 2. At this level the pedicel and its wing-like lateral extensions show considerable irregularity in form.

The low position of the tissue-filled lateral keels of the sporangia is shown on plate 1, figures 3 and 4; also on plate 2, figure 4 (SpK). Plate 4, figure 3, shows a sporangium with but one lateral keel (SpK). The sporangial keel turns sharply upward at the distal end of the sporangium as shown in text figure 2. Radial sections, as on plate 1, figures 1 and 2, and plate 2, figure 2, cut the keel near the apex of its distal upturn and permit a somewhat better visualization of this structure.

The megaspores shown in the sections previously discussed appear flattened or even concavo-convex (cf. plate 1, figs. 1-4). Spores as shown on plate 4, figures 2 and 4, are cut obliquely so that the proximal concavity is not shown. Numerous megaspores have been isolated from the matrix by dissolving the calcite in dilute hydrochloric acid, and these spores illustrate best the original spore form. The proximal aspect of three of these isolated spores is shown on plate 2, figure 5 a-c. The trilete apparatus is seen with the three segments slightly upraised and the sutures split apart. Not all the apical prominence is due to opening of the spores, as there is a distinct natural bulge of the spore coat in the apical region. In general, however, the proximal surface is more or less concave, despite this apical convexity. A scaly "ramentum" which separates easily from the spore coat generally covers each spore. There are no spines on the spore coat such as are characteristic of *Mazocarpon shorense.* The nature of the ramental cover *(R)* is clearly shown on plate 2, figure 1, where it is continuous with the intrasporangial tissue. The cell walls of the intrasporangial tissue adjacent to the developing megaspores have been impregnated with waxy spore-coat material and are more or less incorporated in the outer part of the spore coat. Thus the ramentum seen on these isolated spores is different in origin from the emphytic ornamentation usually seen on lycopod megaspores. The spores themselves must be considered as essentially levigate. Surface features of isolated spores freed of the "ramental" layer are seen on careful inspection to be similar to the surface features of spores generally identified as *Triletes (Aphanozonati) reinschi.* Therefore in McLeansboro coals, *Triletes reinschi,* in part, is accordingly believed to represent *Mazocarpon oedipternum.* As stated in an earlier paper (Schopf, 1938) *T. reinschi* is a generalized form and this species, typically based on isolated spores, probably would include several species if details of the cone structure could be characterized in each instance.

Female gametophytes are present in several of the spores. All cones thus far discovered which contain such "viable" megaspores are in stages of disintegration. A part of one of these cones is shown on plate 4, figure 1. It seems likely that gametophytes developed, as a rule, after the cones had dropped from their parent plants and were lying free in the litter of the coal swamp. No kinetic mechanism can be recognized which would expel the megaspores from the cone or from the sporangium. The prismatic layer is thin on either side of

the pedicel attachment, and this is where the sporangium breaks loose first (compare pl. 1, figs. 2 and 4). Two or three other thin areas, as shown in plate 2, figure 4 (T), also seem to mark natural lines of weakness where breaks in the sporangial wall can easily occur.

The female gametophytes agree in general with those of *Selaginella* and *Isoetes* except that only a single very large archegonium is produced in each megaspore. Proximally toward the apices and around the individual archegonia the cells are smaller and more delicate, as shown on plate 4, figure 5, and also in figures 2 and 4. In figure 2 the gametophyte is somewhat fragmented within the megaspore coat, but the tissue that remains has been transformed into material having all the characteristics of fusain and is fairly well preserved. A single archegonium is also present, although the section illustrated cuts it tangentially and its full diameter is not shown. Plate 4, figure 4 illustrates another megaspore which is similar in most respects but shows the gradation in gametophytic cell size, distal (largest) to proximal (more delicate cells), the best of those shown here. This gametophyte apparently shrank away from the distal spore coat before becoming partly fusainized and mineralized. Figures 8 and 9, plate 3, represent a section across the apical prominence of a megaspore and an archegonium which is cut above the middle so that its full diameter is not shown. A spherical red humic body, somewhat suggestive of an egg nucleus, lies in the center of the archegonial cavity. Figures 5, 6, and 7, plate 3, show part of a series of longitudinal sections through an archegonium. Figure 5 illustrates a median section which shows that the archegonium is pyriform, with a very short neck that protrudes slightly into an external cavity, or vestibule, just below the spore coat apex. A deposit of dark humic material partly fills the venter of the archegonium and obscures some of the cellular details. The venters average about 250 μ in transverse diameter, being much larger than those known in other fossil or modern cryptogams, few of which attain a diameter of 100 μ. Gymnospermic archegonia are generally more than twice as large, but it appears that the largest cryptogamic archegonia known are these from *Mazocarpon.*

In two instances a small globular group of 8 to 12 cells was observed which may represent young embryos within apical cavities that may accordingly correspond to venters of archegonia after fertilization. These are shown on plate 3, figures 1 and 2. Figure 3 shows the structure in figure 2 at lower magnification. The spore from which figure 1 was obtained is the same as that illustrated at lower magnification on plate 2, figure 3. Since gametophytic tissue is not preserved except near the apex of these spores, and since the globules of 8 to 12 cells mentioned show no differentiation of tissues, one cannot be certain of their embryonic nature. If the two respective cellular globules do represent embryos, the original archegonial cavities must have shrunk by inward proliferation of cells, since both the apical cavities are smaller than in normal prefertilization archegonia. The available series of sections demonstrates that the "embryonal" group of cells shown in figure 2 is free of any attachment to the wall of the cavity which surrounds it. The fact that two similar "embryonic" globules have been found shows at least that these structures should not be dismissed as meaningless.

Microsporangiate cones which are identified as forma *microphorum* are shown on plate 5, figures 1 and 3. The first represents a longitudinal and transverse section at the tip of a cone. The cellulose peel from which this photograph was taken extended over both transverse and longitudinal surfaces so that the register of structure in the two opposite planes is perfect. Figure 3 is a similar peel taken at the base of another cone. Although most of the sporangial walls are broken at one or two places, the majority of the microspores have remained in place. This is fairly common in this material, in contrast with the usual condition of preservation of *Lepidostrobus* in which the spores usually have been shed. Some

microsporangiate cones of *Mazocarpon* are more fragmented, and the spores are more or less completely dispersed. Dehiscence of the microsporangia is somewhat more regular than in the megasporangia. A fracture occurs on either side of the microsporangium (corresponding to a position slightly above the lateral keels of the megasporangium) and crosses around over the distal end, as shown by breaks in the sporangial wall in text figures 3b and 3c. It is also common for the microsporangium to separate from its pedicel and split along the line of attachment. It seems probable that the microsporangiate as well as megasporangiate cones were intact when shed from the trees which bore them and that the distribution and association of microspores with megaspores took place in the surficial litter of the peat swamp. Isolated microspores are very common in the matrix of these Calhoun coalballs, and if wind had been an effective agent in their dispersal, it does not seem that the microspore concentration would be so great.

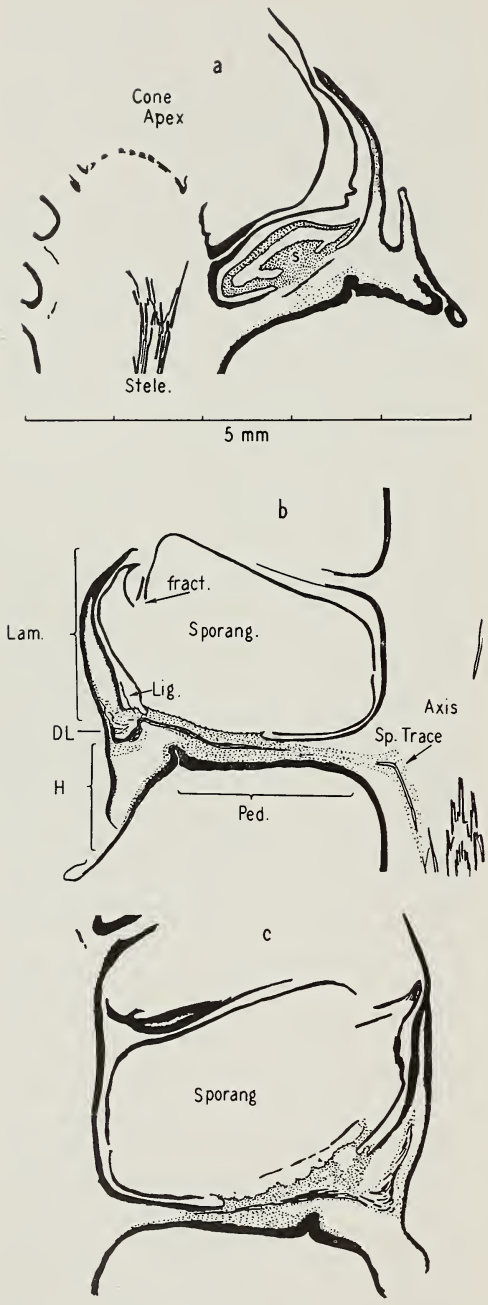
Microspores are shown at higher magnification on plate 5, figure 4. They are about 60 μ in diameter, slightly triangular, with trilete rays extending to the equator. The exospore is papillate, as shown in figure 4a. The endospore is thin but generally distinct. The exospore is commonly torn when the peels are removed, the endospore remaining intact, as in figure 4b. The sutures are carried through the endospore, and at the tip of each of the endosporal pyramic segments there is a refractive globule or thickened spot. This is characteristic although its significance is unknown. The endospore shows no other distinctive features.

The microsporophylls shown in figure 3, plate 5, seem unmistakably to be in verticils. The slightly tangential section of the cone apex shown at greater magnification on plate 5, figure 5, illustrates the nearly perfect symmetry on either side of the cone axis.

In contrast to *Mazocarpon shorense* and *M. pettycurense*, *M. oedipternum* has very little sterile tissue in its mature microsporangia. In immature sporangia a moderate amount of sterile tissue is found, as shown diagrammatically in text figure 3a from a sporangium at the tip of a cone. The subarchesporial pad of mature sporangia collapses into an irregular line of material centrally located in the sporangium which is sometimes "T" shaped as shown in figure 6, plate 4 (s). This is connected to the pedicel along the line of sporangial attachment. The walls in mature microsporangia, like the walls in the sporangia of most other lycopods, are only a single cell-layer thick. There is little if any more sterile tissue in these microsporangia than in those of several species of *Lepidostrobus*.

The presence of the ligule is very difficult to ascertain on most of the sporophylls. Ligules are rarely found, which is surprising in view of the abundant and well-preserved material available. No ligules have yet been found at the cone tip, and it is certain that the ligules did not function as protective organs for the apical meristem, as the sporophyll laminae themselves overarch the meristem and provide this protection (pl. 5, fig. 5). It is still possible the ligule may have functioned in sporelings during germination stages. Plate 4, figure 7, shows what is probably the shrunken vestige of a ligule (lig). The distal end of this sporophyll is shown at lower magnification in figure 8 and is also drawn diagrammatically in text figure 3b. In some megasporangiate sporophylls there is a suggestion of a pit distal to the sporangium which may represent a place of ligular attachment. However, from the evidence now at hand one hesitates to say that the ligule is a constant feature of either megasporangiate or microsporangiate sporophylls.

As previously mentioned (p. 14) the sporophyll trace in the pedicel and lamina is chiefly composed of scalariform tracheids. Distal to the sporangial attachment and above the heel, the trace curves downward abruptly before it turns up to supply the lamina. This distal downturn of the trace has been called a "dorsal loop". Inside the loop the trace expands by the addition of scalariform transfusion-type tracheids. These are shown in figure 7, plate 4,



and are also indicated diagrammatically in text figures 3b and 3c inside the dorsal loop (DL). The trace follows along the upper part of the pedicel but does not enter the ridge of tissue which attaches the sporangium, nor does there seem to be any special development of transfusion tracheids on the ventral side of this portion of the trace (see plate 6, fig. 7) although food must have been actively transferred along this line during sporangial development. Lack of ventral transfusion tracheids in the sporangial attachment is in contrast to the condition described for *Mazocarpon shorense*. The traces while still in the cone axis contain a large number of characteristic spiral and annular elements such as are shown on plate 6, figure 8. The traces originate from the stele at an acute angle and connect there with exarch spiral and annular protoxylem elements. Plate 6, figure 5, shows an extreme tangential section of a stele which includes one of these protoxylem groups. The stelar metaxylem is made up of somewhat larger scalariform elements as shown in figures 4, 6, 9, and 10 of plate 6. In many specimens the stele contains a pith, composed of prosenchymatous cells (fig. 6). Generally a few isolated tracheids, apparently annular, are dispersed in the central tissue of these steles (figs. 9 and 10). In some cones the zone of metaxylem is relatively thick with a corresponding decrease in the amount of medullary tissue (fig. 4), and occasionally the pith is absent (fig. 3). The primary protoxylem points seen in cross-sections vary from about 10 to 12. Their arrangement indicates a spiral sequence in some specimens but more commonly a verticillate arrangement (fig. 10). There seems no reason for assuming that the number of protoxylem points is invariable or that the phyllotactic arrangement of sporophylls is inflexible.

Fig. 3a.—Outline tracing of immature microsporophyll at cone tip. Dark borders indicate the extent of subdermal sclerotic tissue and sporophyll trace. Thin-walled tissue stippled. s=subarchesporial pad. From C. B. 124 E (27).

b.—Outline tracing of median section of ripened microsporophyll showing sporangium (Sporang.) still containing microscopes but with wall broken (fract.), its attachment to the pedicel (Ped.); the sporophyll trace (Sp. Trace) with its dorsal loop (DL); the ligule (Lig.), lamina (Lam.), and dorsal heel (H). From C. B. 124 E (32).

c.—Outline tracing of median section of ripe sporophyll as given above in *b*. The lamina is slightly longer than usual. From C. B. 124 E (27).

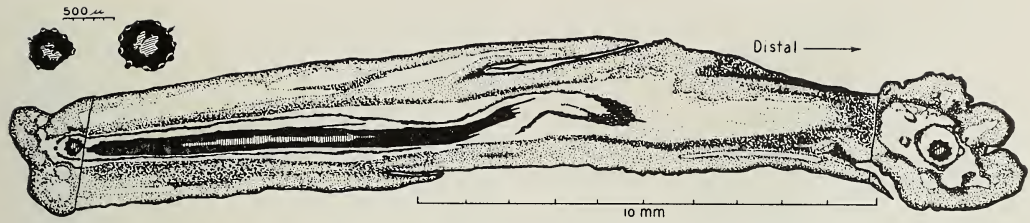


FIG. 4.—Segment of peduncle of (?) *Mazocarpon oedipternum*. Drawing was prepared from a peel taken simultaneously from tangential and transverse surfaces as shown. Proto- and metaxylem of stele shown in black; medullary tissue lined; cortical tissue stippled. Steles are separately drawn at higher magnification at the left to show protoxylem points. From C. B. 136 A5 (17).

The peduncle of a cone is illustrated on plate 6, figure 2, and in text figure 4. The axis illustrated was not found attached to a cone but the close similarity of its stelar structure to that of less well preserved but attached peduncles permits little doubt as to its relation. The stele of another peduncle is shown at greater magnification on plate 6, figure 1. Were it not for the stelar similarity, there might be some doubt as to the identification of the peduncle because of differences in the cortical tissue. The cortical tissue is rather thick at the position illustrated by figure 2 and shows prominent parichnoidal cavities. Adjacent to the cone, however, there seems to be a definite transition to the structure of the cone axis; the peduncle is smaller than in figure 2, has no bracts, and the outer surface is quite regular. At this higher position close to the cone, sclerenchyma is present around the periphery which presumably merges proximad with the thick outer cortical tissue of the peduncle. In the cone axis the thick sclerotic cortex is largely absent. The peduncle is nearly bare adjacent to the cone, but proximally it bears a number of short bracts in an irregular spiral arrangement as shown by the segment illustrated in text figure 4. The bracts, as shown by transverse sections of the two ends of this segment, obviously vary in their arrangement. The drawing (text fig. 4) was prepared from a peel which covered both of the transverse surfaces and one tangential surface so that the structure in both directions is continuously related, but the proximal end is sectioned at a deeper tangential level than the distal end. The dimensions of the peduncle increase slightly away from the proximal end.[5] A greater number of bract bases are transected at the distal end and the stele is somewhat larger there with more protoxylem points. Orientation is proved by the manner of attachment of the bracts. Steles from both ends are diagrammatically represented at higher magnification at the left of the text figure. The pith area is invaded somewhat by medullary tracheids as in the cone axis.

A more complete account of the variations in the peduncle cannot be presented at this time. Additional study is needed since the structure of the peduncle is particularly important in establishing the relationship of *Mazocarpon* with better known genera identified on the basis of stem structure. It is a matter of interest that a ligule appears to be present in the axil of one bract shown in nearly median section in text figure 4.

[5]The form that Lesquereux first named *Lepidostrobus lacoei* (1880, p. 439), later referred to *Lycopodites* (1884, p. 780), which is illustrated in vol. III of the Coal Flora (pl. CVII, fig. 1) is of interest. It appears to have no connection with either *Lepidostrobus* or *Lycopodites* and instead is properly referable to *Sigillariostrobus*. This genus, as mentioned later, compares favorably in several respects and is intimately related to *Mazocarpon*. Lesquereux's specimen apparently shows the complete peduncle which in this case is devoid of bracts except for a few near the base of the cone. The peduncle varies in diameter from about 7½ mm. at the proximal end (where it presumably was attached to the trunk of the tree) to about 4 mm. near the middle from whence it again expands to about 8 mm. in diameter at the cone base. In all it is about 14 cm. in length. The peduncles of *Sigillariostrobus goldenbergi* (cf. Zeiller, 1884, pl. 12, fig. 5) and of other species of *Sigillariostrobus*, while often less complete, also show some indication of a similarly inconstant diameter. The seemingly anomalous feature shown by a sector of peduncle of *Mazocarpon oedipternum* in text figure 4, with a distal diameter greater than the proximal may thus be in general agreement with peduncles of other cones of sigillarian affinity.

COMPARISON OF *M. OEDIPTERNUM* WITH OTHER SPECIES OF *MAZOCARPON*

Mazocarpon pettycurense Benson (1918).—This species from the Lower Carboniferous Calciferous Sandstone is geologically the oldest species known. Information in regard to it is scant (Benson 1908; 1918, p. 578; and Scott, 1920, p. 216). The only illustrations are the drawings given by Miss Benson in connection with her discussion of the sporangiophore (New Phyt. fig. 25, 1908). The chief distinction upon which this species is based is that the apiculate megaspores are more numerous than in *M. shorense* and other species. From Miss Benson's figures it may also be inferred that the definite arrangement of megaspores in the sporangium and the spore form characteristic of the Pennsylvanian species, had not yet been established when the Calciferous Sandstone sediments were deposited. A large amount of intrasporangial tissue is definitely shown for both megasporangia and microsporangia of *M. pettycurense*. The megasporangium apparently lacks lateral keels, and this also may be an identifying characteristic.

Miss Benson notes later (1918, footnote, p. 579) that the microsporangium of *M. pettycurense* (1908, fig. 25b) is magnified 30 times, whereas the megasporangium (fig. 25a, 1908) is magnified 39 times, but the two are drawn as if they were the same size. This is a difference in actual linear dimensions of about 23 per cent, the microsporangium being the larger. Whether this is an actual size difference or whether the sections were merely from different tangential positions on the cone cannot be judged.

Mazocarpon cashii (slide 472A, Manchester Collections).—This species is probably of Lower Coal Measures (upper Lanarkian) age, although the source of the type specimen is not definitely known. It is said to be distinguished from *Mazocarpon shorense* by the sporophyll traces in the cone axis which "are surrounded by a sheath as they pass out through the lacunar middle cortex" and by transfusion tissue at the base of the megasporangium which is "more highly differentiated". Miss Benson's illustrations of *Mazocarpon cashii* (her figs. 15, 16, and 17) also seem to indicate a form somewhat smaller than *Mazocarpon shorense*. However, *Mazocarpon cashii* is not well enough characterized at present to offer any adequate basis for comparison with *M. oedipternum* beyond that presented with regard to *Mazocarpon shorense* which, in any event, is very closely related to it.

Mazocarpon shorense.—This species is much better known than either of the other English species, since it is the form chiefly dealt with in Miss Benson's paper of 1918. It was obtained from the Great Coal-ball horizon (Halifax Hard Bed) and from the Hough Hill and Stalybridge coal which is slightly older. It also has been recorded comparatively from the Finefrau-Nebenbank coal in Limberg, Holland, by Koopmans (1928, p. 21). It thus appears to be a fairly common and widespread form which, as far as is known, is restricted to the lower Westphalian A. A detailed description of *M. shorense* has been prepared, summarized from Miss Benson's account (1918) and given below, in order that a close comparison can be made with *M. oedipternum* previously described. Where measurements were not originally provided by Miss Benson, they have been obtained as far as possible by measurement from the published illustrations. Attention is called to a few discrepancies and to points where additional information would be helpful.

Cones pedunculate, 13.5 mm. in diameter, more than 8 cm. long. It is not definitely known whether or not cones were unisexual. Sporophylls are characteristically deciduous in their entirety; arrangement on the cone axis is stated to be in a "close spiral" but the arrangement also may have been verticillate. Cone peduncle and axis somewhat hexagonal, about 3 mm. in diameter, outer sclerotic tissue relatively thick (slightly under a millimeter). Mesarch sporophyll traces and associated tissues pass through sclerotic tissue on a rather long slant. Stele apparently medullated, about ½ mm. in diameter, with projecting protoxylem points; other details unknown. Sporophyll pedicels diminish in width to about 1 mm. at their point of attachment to the cone axis. Pedicel extends radially for about 5 mm. and

merges there with the upturned lamina. Lamina rises to the third rank above, hence was probably about 10 mm. long. Lamina is about 6 mm. broad and spoon-shaped at its base; laminal outgrowths on either side of the pedicel are not as broad as in *M. oedipternum*. Dorsal heel nearly lacking; sporophyll is thickened at the juncture of lamina and pedicel but extends downward only about 8/10 mm. below the plane of the pedicel. (Cf. p. 580, op. cit. It is evidently a mistake where it is stated, op. cit. p. 576, that this "convex cushion might be 8 mm. below the plane of the keel.") Megasporangium is about 5 mm. in length, 2.6 mm. in height, and attached to a ventral ridge of the pedicel. Traces of a ligule are reported situated in the sinus distal to the sporangium. The sporophyll trace extends the length of the ventral ridge instead of in the pedicel itself and recurves downward at the distal end to enter and supply the lamina. The sporangium is somewhat narrower adjacent to the axis and broader distally. Externally it is marked by a keel ("sporangial lamella") extending on the sides and around the distal tip of the sporangium. Position of the keel on the sides of the sporangium is somewhat uncertain. Miss Benson's much copied text figure 1 (op. cit. p. 571) shows the keel recurved upwards and only carried toward the axis about midway, high on the side of the sporangium. Her photographs of tangential sporangium sections (figs. 1 and 16, pls. XVII and XVIII, op. cit.) show the keel low on the sides. It would seem probable that the photographs show its position more accurately. The sporangium and its keel are covered externally with a characteristic prismatic cell layer. As many as eight large (about 2 mm. diameter), radially symmetrical, plano- or concavo-convex, strongly apiculate megaspores are contained in each megasporangium. The spores are in a definite arrangement around the periphery, with their apices oriented toward the center of the sporangium. Intrasporangial tissue fills the central part of the sporangium, more or less encloses each of the megaspores, and marginally lends rigidity to the sporangial wall. External to the megaspores this tissue is only a few cells thick except in spore interstices and in the sporangial keel. Some megaspores, either isolated or in partially disintegrated sporangia, possess gametophytes. At least two archegonia may be produced subjacent to the spore apex. From Miss Benson's plate XVII, figure 3 (op. cit.) the venters appear to be at least 200 μ in diameter.

The details of the male cones (or portions of cones?) and of the microsporangia are much less satisfactorily known. It seems

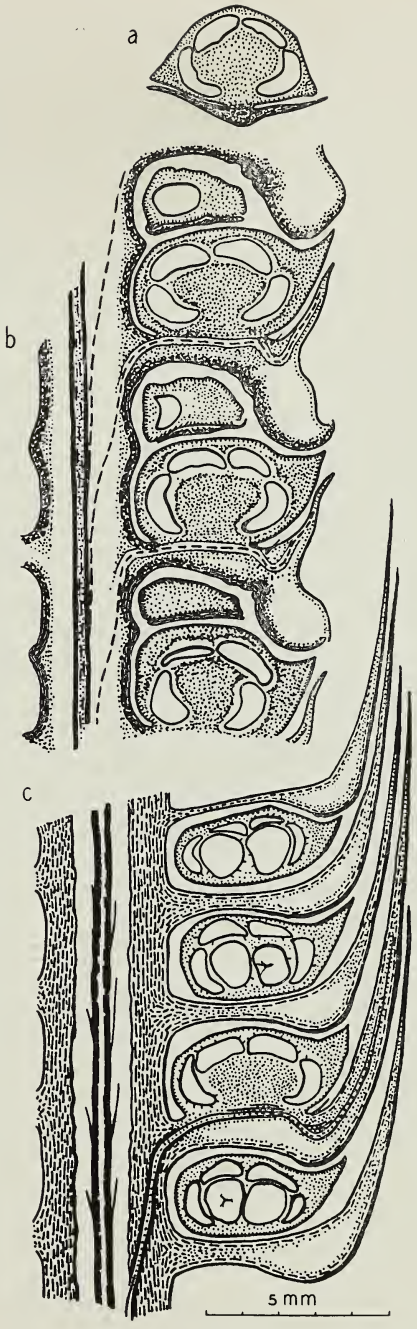


FIG. 5.—Diagrammatic representation of *Mazocarpon oedipternum; a*, megasporophyll in transverse section near the middle; *b*, portion of megasporangiate cone in longitudinal section; *c*, diagrammatic representation of *Mazocarpon shorense;* based on information summarized from Miss Benson (1918). Diagrams *a-c* drawn to the same scale.

that spores were produced in pockets of massive intrasporangial tissue. The single microsporophyll found was evidently immature since the spores were still in tetrads. Tissue-filled sporangial keels are present. These features and the association of this specimen with megasporangiate material in coal-balls from Shore, Lancashire, are the basis for assigning it to *Mazocarpon shorense.*

The features of the megasporangiate cone of *Mazocarpon shorense* (text fig. 5c) and of a similar cone of *M. oedipternum* (text fig. 5b) have been incorporated in diagrammatic longitudinal sections for direct comparison. Besides the great difference in thickness of the axial outer cortex and in length of their respective sporophyll laminae, the diversity in spacing of sporophylls may be noted. *M. shorense* is here depicted with the sporophylls in a "close spiral" and the distal "convex cushion" (heel) close above the sporangium below. The sporophylls of *M. oedipternum* are more widely and alternately spaced. Wide spacing of the sporophylls is apparently connected with formation of the large dorsal heel of *M. oedipternum.* No causal explanation for this phenomenon can be advanced at present. The heel serves to make the cone more rigid (as it does in *Lycopodium cernuum,* see Lang, 1908) but if the sporophylls were more closely mounted on the axis, as in *M. shorense,* presumably the same degree of rigidity would be achieved without a dorsal heel.

There seems to be little essential difference between the megasporangia of *M. shorense* and *M. oedipternum.* The latter species, however, lacks the upstanding ventral pedicel ridge which attaches the sporangium of *M. shorense.* In the new species the vascular trace runs close to the top of the pedicel for part of its length but can not be said to leave the pedicel. Thus far no vascularization of the base of the sporangium has been noted such as was reported for *Mazocarpon cashii* and in lesser degree for *M. shorense.* Consequently, no additional support is given the sporangiophoric interpretation once advanced by Miss Benson (1908). The centrally located intrasporangial tissue in the megasporangium of *M. oedipternum,* which may be compared with the subarchesporial pad of modern lycopods, shows a slight alignment of cells radiating from the base. This may be a result of growth of intrasporangial tissue in the direction of the nutritional gradient while the young sporangium was actively enlarging.

The levigate megaspores of *Mazocarpon oedipternum* are distinct from the apiculate spores of *M. shorense.* Probably of greater significance is the fact that more than one archegonium may be produced within a single megaspore of the English species. *M. oedipternum* has been found in about a dozen instances to have only a single very large archegonium placed directly below the spore apex. This is a rather surprising constancy in a character which is variable in modern forms. Although it is a member of the Paleozoic flora it seems more advanced and specialized in this feature than either modern *Selaginella* or *Isoetes.* The large size of the archegonia also is probably a specialized feature. The gametophyte and archegonia are far better preserved in *M. oedipternum* than are those from any other Paleozoic form now known.

The microsporangiate cones of *M. oedipternum* are considerably different from those ascribed to *M. shorense.* They differ little from microsporangiate portions of cones of *Lepidostrobus,* the chief specific distinction apparently being the broad lateral laminae of the pedicel in *Mazocarpon oedipternum*; the pedicel of *Lepidostrobus* sporophylls is, in comparison, very contracted. The microspores of both *M. oedipternum* and *M. shorense* are exceptionally large for lycopod microspores. Whether features other than size are similar is indeterminable at present because the *M. shorense* microspores were all in tetrads and lacked their mature ornamentation.

RELATION OF *MAZOCARPON* TO AFFILIATED GROUPS OF PLANTS

The genera to be considered are: (1) *Sigillaria,* a group of plants identified by diagnostic characteristics of their stems; (2) *Sigillariostrobus,* a group of plants identified by certain features of their cones, generally discernable when preserved as impressions and coalified compressions; and (3) one section of the genus *Triletes,* the *Aphanozonati,* a group of lycopods identified by certain characteristics of their isolated megaspores. *Mazocarpon* is a group of plants identified by certain specialized characteristics of cones and sporangia which may be distinguished only when well preserved. The groups overlap in a biological sense and can be represented as members of the *Sigillariaceae* during a considerable part of Carboniferous time. However, the degree of overlap between the genera or species is not precisely definable. The relationships of the late Devonian and early Mississippian antecedants are obscure, and post-Carboniferous representatives are also inadequately known. Chiefly because of the inadequacy of knowledge of specific interrelationships during Pennsylvanian time and generic and suprageneric interrelationships during the late Devonian and early Carboniferous time it appears necessary to classify the diverse fossils separately, in different specific and generic groups at least. Treated thus, the minor stages of the evolutionary sequence may be discussed more readily and accurately; nomenclatorial confusion can be reduced to a minimum because probable interrelationships are referred to more precisely.

Information obtained from the study of *Mazocarpon oedipternum* supports the belief that the different genera mentioned above are all members of an intimately related series. It seems that the major line of phylogenetic affinity is reasonably certain even though the minor stages of evolution are imperfectly known. The object of further study should be the recognition of these minor stages of the evolutionary sequence, keying them carefully with the time sequence represented by the sedimentary strata. Study of the abundant megaspores will aid greatly. In the past, sigillarian fructifications have been identified less frequently than their stems, and it has been a question whether some of them were most intimately allied with *Lepidostrobus* and other lepidodendrids rather than the sigillarians. If this were the case, an interlocking phylogenetic relationship between the lepidodendrids and sigillarians might be indicated. The two groups are for the most part easily distinguished by characters of the leaf bolsters, but there has always been some question whether these distinctions were of actual generic importance, and if so, at what point in the geological history generic segregation took place. The presence of *Mazocarpon* at a position rather high in the Pennsylvanian shows that the characters which distinguish *Mazocarpon* from *Lepidostrobus* were important and persistent, and shows that direct phyletic connection between these two lines in Pennsylvanian time is improbable. It is more likely that the two groups diverged in the early Mississippian.

In the following discussion, important characters in classification of the sigillarian alliance are considered. The object is to illustrate the relationship of these forms in the light of reconsideration of certain of the significant biocharacters. It seems that more emphasis may reasonably be placed on some of them, such as mode of fructification and character of the megaspores, than has been generally recognized. On the other hand, the characters of cone phyllotaxis appear to have been overemphasized.

The manner in which the cones are borne on these plants seems to be a character of major importance in definition of the sigillarian alliance. Both *Mazocarpon* and *Sigillariostrobus* cones are pedunculate, and stems of *Sigillaria* bore fructifications on the main trunks by means of peduncles. A primary

characteristic of *Sigillariostrobus,* distinguishing it from *Lepidostrobus,* is that cones in the latter genus are terminally attached to ordinary leafy twigs, whereas in *Sigillariostrobus* the cones are borne on the specialized peduncles. The general correlation of such cones with sigillarian stems showing the scars where cone peduncles were formerly attached is adequately supported. At a few horizons (cf. Zeiller 1884) even a specific correlation of stems and cones has been attempted. The specific evidence is not altogether conclusive, however, and even if it were, the pertinent question as to the duration in coincidence of certain specific features of the cones with other specific features of the stems would still be unanswered. The correlation of *Mazocarpon* with *Sigillaria,* is based on evidence comparable to that which applies to *Sigillariostrobus.*

The manner in which cones of *Lepidostrobus* are borne is similar to that found in modern *Selaginella* and more advanced species of *Lycopodium.* This mode of fructification nevertheless is far more primitive, so far as relative specialization is concerned, than the pedunculate manner of fructification noted in the sigillarians. Variations of this sort are recognized as important wherever they are noted in study of modern plants; they probably are similarly reliable indicators of specialization in the Paleozoic flora. The specialized fruiting habit of Pennsylvanian sigillarians seems well established and, in conjunction with other advanced features, may be taken to indicate that this sigillarian alliance represents an entirely distinct group of lycopods during the Pennsylvanian period.

Whenever evident, peduncle scars generally occur abundantly in short zones upon the stems of *Sigillaria.* This may be taken to indicate some sort of periodicity in fruiting. Whether it was coordinated with climatic or seasonal periodicity, like the growth ring specialization of modern plants, is unknown, but it is reasonable to suppose that it was at least connected indirectly, indicating specialization which is not as distinctly shown by other groups of Paleozoic lycopods.

Information is scant in regard to the fruiting habit of Lower Carboniferous sigillarians. It would be expected that at some time in the early history of the groups, specialized cone-bearing peduncles would be much less in evidence. No knowledge of the cone axis or peduncle of *Mazocarpon pettycurense* is available. If it should prove to be nonpedunculate, its generic segregation from *Mazocarpon* might be advisable. It is evident that the fruiting habit of Pennsylvanian sigillarians is a heritable and consistent characteristic which is at least of generic significance.

Stems of the sigillarians may not indicate conclusively the mode of fructification, due to the unequal distribution of peduncle scars. Consequently this character is of less practical value in classification of stem specimens, but the peduncle is often shown by good specimens of cones and is more useful in their classification.

Proof of the real overlapping relationship of *Sigillariostrobus* with *Sigillaria* has been most convincingly shown by Zeiller. Cone peduncles bearing acicular bracts and bract-scars which resembled those on certain associated *Sigillaria* stems seem to be fairly conclusive. It now appears (relying on descriptions extending over about a century) that more emphasis can be placed on lack of conflicting evidence than on the positive evidence which supports this general conclusion. Existing evidence is based on association and on resemblance between peduncle bract-scars and stem leaf-scars—a comparison which probably is not altogether satisfactory because the bracts and leaves were not entirely similar and no doubt produced cicatrices which were somewhat different, even on the same plant.

Proof of a similar relationship between *Mazocarpon* and *Sigillaria* is derived chiefly from comparison of peduncular steles preserved within sigillarian stems and in *Mazocarpon* cone axes and peduncles. This relationship in no way conflicts with other information pertaining to the relationship of *Sigillariostrobus.* The basis for considering that *Mazocarpon* possesses the same sort of relation to *Sigillaria* that

Sigillariostrobus does, is best indicated by reference to the few important papers which describe the structure of peduncle steles within petrified stems of *Sigillaria.*

PEDUNCULAR STELES OF *SIGILLARIA* AND *MAZOCARPON*

In 1926 Hagéne described a section of a ribbed sigillarian stem from the paleobotanical collections of the University of Lille. This specimen apparently had been collected and prepared by Hemingway in England. The collection locality was given as "Colne, Lancashire," from the horizon of the Halifax Hard Bed coal,[6] and Hemingway had labeled it "*Sigillaria elegans*". This stem is unique in that it is one member of the Favularian section in which the rather large stele does not possess any secondary wood, and further, in that a large number of small steles, some of which are solid and others medullated, surround the main central cylinder. Numerous leaf traces, single and bar-like near the stele but double in the inner cortex, are also present. Characteristic sigillarian leaves with corresponding double vascular strands are also associated in the same section. The peduncular steles are of chief interest, for from them Hagéne concludes (op. cit., p. 113, free translation) that "this specimen both establishes the structure of the bundles destined for fructiferous peduncles and *confirms the relationship between the genus* MAZOCARPON *and the genus* SIGILLARIA". His conclusion apparently is based on the close agreement between the medullated peduncle steles shown in his section and the peduncle stele in the *Mazocarpon shorense* cone axis illustrated at low magnification by Benson in 1918. There also is a good general resemblance between the medullated steles adequately figured by Hagéne and those in *Mazocarpon oedipternum.*

Hagéne's paper is significant and excellently illustrated, but it seems to have been overlooked by later authors. Hirmer (1927) makes no reference to it. Miss Calder (1934) also overlooked it in describing two sections from the Kidston collection which seem to have been taken from the same Colne specimen. The collection data given by Miss Calder agrees with that previously given by Hagéne. She reports that the external characters of this stem were exhibited prior to sectioning, and Mr. Hemingway informed her that its identification as *Sigillaria elegans* was confirmed at that time by Kidston. Miss Calder's description in the main agrees with that of Hagéne. However, she describes the solid stelar appendages as pertaining to cone peduncles and is undecided as to the nature of the small medullated steles; she makes no reference to *Mazocarpon.* It seems unfortunate that sections of this excellent specimen were allowed to become separated. Not only was there duplication of effort, but neither author was able to make a first-hand evaluation of all the evidence. Probably additional information could have been presented had this been possible.

Graham (1935, pp. 158-161) described a stem from Calhoun coal-balls which he assigned to *Sigillaria approximata* Font. et I. C. White. Peduncular nonmedullated steles are quite numerous in sections of this stem but Graham reported none of the medullated type of vascular cylinders found in *Mazocarpon oedipternum.* The solid steles he described are somewhat smaller than the solid type steles also present in *M. oedipternum* cone peduncles. Some of the *Mazocarpon oedipternum* cones possess a solid stele, but there is little evidence now that specifically similar cones were borne by Graham's *Sigillaria approximata,* even though both species are from the same horizon. The stem structures described by Graham agree in general with those first reported from *Sigillaria elegans* by Kidston (1904), but probably internal as well as definite external differences can be found.

The histological structure of *Sigillaria elegans* (not to be confused with the Permian form, *Sigillaria menardi* which

[6]Stopes and Watson indicate that coal-balls occur at Colne, Lancashire, in a coal below the "First Grit" and presumably different from the Hard Bed horizon. It is thus uncertain, to the author at any rate, whether the Colne *Sigillaria* is from the Great Coal-ball horizon or one slightly lower in the Lanarkian.

was described as "*S. elegans*" by Brongniart in 1839) was first described in adequate detail by Kidston in 1905 from a specimen found at the Great Coalball horizon in England (the same as *Mazocarpon shorense*). The peduncular steles described within the stem were apparently not similar to those in specimens of *M. shorense*, and no comparison has been made between the structures of the two. Kidston's description was drawn from sections of only two peduncles, and it seems that the Colne specimen with many peduncular steles provides a more accurate picture of the variation possible in these structures. Apparently none of Kidston's original sections passed directly through a zone of the stem which bore numerous cones. It would seem that the differences between the peduncular steles of Kidston's specimen are easily reconciled with those shown by *Mazocarpon* now that both solid and medullated steles are known in the later genus.

Mazocarpon oedipternum shows that *Mazocarpon* may have both solid and medullated steles within the limits of the same species; the Colne *Sigillaria* shows that both types of peduncular steles may even be formed within the same plant. The presence of a solid type of peduncular stele in Kidston's original specimen of *Sigillaria elegans* and in Graham's *Sigillaria approximata* is not discordant with the belief that *Mazocarpon* type of cones were borne by *Sigillaria*. In the absence of conflict in these more precise characters and in the agreement of other more general information, the fact of a generic overlap seems sufficiently founded. On the other hand, there is no very convincing specific agreement in peduncular structures of any of the species of *Sigillaria* or *Mazocarpon*. This is not surprising in view of the few descriptions of *Mazocarpon* and other sigillarian cone peduncles which have been published. The inherent variation in peduncular structure may in itself be regarded as a generic character, and such variation in any event renders specific correlations more difficult. This emphasizes the necessity of classifying in separate groups the fossils identified by characteristics of their cones and those identified chiefly on characteristics of their stems. In each group, other more stable characteristics are present and serve best as means of specific discrimination.

RELATION OF *MAZOCARPON* AND *SIGILLARIOSTROBUS*

In view of the similar relationship which has been suggested between both of these genera and the genus *Sigillaria* it may be expected that the relationship between *Mazocarpon* and *Sigillariostrobus* is particularly intimate and that generic synonymy might exist. The present evidence favors this interpretation; nevertheless, if we are to maintain precision in the application of nomenclature, it is impractical to assign all of the species classified in both groups to any one generic group. On the other hand, it would seem justified to unite them in some larger group, such as a tribe. As stated above, *Mazocarpon* is more precisely definable and is presumably therefore a more satisfactory taxonomic group.

Miss Benson (1918) has previously discussed some of the evidence for believing *Mazocarpon* and *Sigillariostrobus* very closely related and has compared *Mazocarpon shorense* with *Sigillariostrobus ciliatus, S. rhombibracteatus, S. tieghemi*, etc. In view of the additional information made available in *Mazocarpon oedipternum*, the relationship between the two genera may be reexamined with reference to a few important characters, and further discussion may be presented concerning certain species of *Sigillariostrobus*, chiefly those described since Miss Benson's paper appeared.

The diagnosis of *Sigillariostrobus* is still subject to differences in interpretation. By many the name is used to designate cones or cone fragments which are supposed to correlate with *Sigillaria*. But a scientific nomenclature may not be based on suppositions, and at least some of the specimens assigned to this genus in the past must be considered problematic or identifiable only to some group having broader affinity than *Sigillariostrobus*.

A cardinal point in the identification of *Sigillariostrobus* is the pedunculate

mode of fructification, a characteristic whose importance has been emphasized [7] There are certain other features which also must be more or less definitely included in the diagnosis of this genus but none of them seem entirely essential. The cones are of medium to large size. The sporophylls are often apparently in verticils and, so far as is known now, they appear to be unisexual. The megaspores appear to agree with those of the *Aphanozonati* section of *Triletes*. In Schimper's original description of *Sigillariostrobus* (1870) he assumed that the smaller of the spores were microspores although they were about a millimeter in diameter. Consequently he considered the cones of *Sigillariostrobus* heterosporous. Several authors have commented that all the spores described by Schimper are probably megaspores, and this is apparently the case because features of even the smallest of the spores he mentions agree with known megaspores, and of all the lycopod microspores known none exceed 1/10 the diameter of the "microspores" Schimper observed.

So far as size and general habit characteristics are concerned, the cones of *Sigillariostrobus* are not different from *Mazocarpon*. The cones of *Mazocarpon* thus far described are all smaller than the largest of *Sigillariostrobus* species, but the majority show marked similarity if allowance is made for differences in preservation.

Bochenski (1936, p. 230) has suggested that verticillate arrangement of sporophylls (in addition to their pedunculate characteristic) may also be a diagnostic feature of *Sigillariostrobus*. There is probably a much greater tendency towards verticillate arrangement in both *Sigillariostrobus* and *Mazocarpon* than in *Lepidostrobus*. This character cannot be considered diagnostic however, since Zeiller (1914) reports a verticillate arrangement of sporophylls in *Lepidostrobus brownii*, and Binney (1871) has also illustrated specimens which are verticillate. Verticillate arrangement in *Lepidostrobus* is harder to establish than in *Sigillariostrobus* or *Mazocarpon* because the orthostiches commonly appear to be more numerous. Still in the lepidostrobid forms mentioned, there seems no occasion to doubt that the sporophylls are in verticils.[8] All these are from the Lower Carboniferous[9] which may be a point of some significance. Most Pennsylvanian species of *Lepidostrobus* seem to have a spiral phyllotaxy. But in any event there is no direct relationship apparent either between verticillate species of *Lepidostrobus* and verticillate species of *Sigillariostrobus* or between *Lepidostrobus* and *Mazocarpon*. It is therefore impossible to consider this character of essential diagnostic significance.

It should also be pointed out that a low spiral phyllotaxy may, under some conditions of preservation, simulate verticillate arrangement or vice versa. The arrangement of sporophylls reported for *Mazocarpon shorense* may easily be as "verticillate" as some specimens of *Sigillariostrobus* in which a whorled phyllotaxy is confidently reported. Even if the possibility of error in determination of phyllotaxy in *Sigillariostrobus* is discounted, the possibility of deviation from a strictly whorled to a low spiral arrangement of sporophylls must always be borne in mind when dealing with this group of plants. Specimens of *Mazocarpon oedipternum* are illustrated which may represent both types. However, so far as phyllotaxy is concerned, *Mazocarpon* and *Sigillariostrobus* here have no points in significant conflict.

There is considerable evidence that cones of both *Mazocarpon* and *Sigillari-*

[7] Kidston (1911 p. 182) has considered the *Ulodendron* condition of Clathrarian sigillarians indicative of the presence of sessile cones in this section (in part); *Sigillaria discophora* which he cites is placed by several authors in the separate genus *Ulodendron*, and in any event Watson (1914) has shown that *Ulodendron* type scars are not caused by sessile cones.

[8] Species of *Bothrostrobus* are also described as verticillate.

[9] Hirmer (1927, p. 230) says *Lepidostrobus brownii* is from the middle Upper Carboniferous but this is an error. The geologic position of several noted specimens of *L. brownii* (including the holotype) is unknown because they were secondarily derived from glacial deposits. Zeiller (1914) gives the age of several specimens whose source is known, as lower Dinantian, i.e., the lower part of the Lower Carboniferous, and Read and Campbell (1939) suggest that some of them may possibly even be from beds of uppermost Devonian age. The source of *L. fischeri*, Scott and Jeffrey, (the name later changed to *Lepidostrobus kentuckyensis* by Scott because "fischeri" was preoccupied) also is listed erroneously by Hirmer; this species comes from the New Albany shale which Read and Campbell (1939) believe also is uppermost Devonian.

ostrobus are generally unisexual. In this connection it is more pertinent to discuss the few reports in which cones of *Sigillariostrobus* have been considered bisexual than the more numerous records in which spores of one type only (generally megaspores) were reported. Seldom has it been possible to prove the unisexual nature of the cones conclusively, although Bochenski (1936) demonstrated that cones of *Sigillariostrobus czarnockii* are undoubtedly unisexual. It is probable that extensive use of similar maceration methods will prove the point more conclusively for other species. In the meantime, the lack of substantial reports of bisexual cones of *Sigillariostrobus* must be taken to suggest that they are unisexual, particularly when this is supported too by the indirect evidence supplied by *Mazocarpon oedipternum.*

The fact that the "microspores" mentioned by Schimper (1870) are actually quite typical megaspores has been mentioned. The next suggestion of bisexual cones of *Sigillariostrobus* is in a paper by Kidston in 1897. In it he illustrates a specimen identified as *Sigillariostrobus* sp. (op. cit. 1897, pl. II, fig. 1) which he thought might possess microsporangia as well as megasporangia. Only the megaspores are actually demonstrated; no microspores or conclusive evidence of microspores was obtained from the purported microsporangia, and the size of imprints of the "microspores" are given as about 200 μ. In the absence of other definite characteristics, this seems too large for actual microspores. The fragmentary cone, in any event, is inadequate as a source of definitive information.

Miss LeClercq (1938) has recently assigned a cone from the Yorkian in England, formerly identified mistakenly as *Sphenophyllostachys,* to *Sigillariostrobus sphenophylloides* n. sp. This cone is undoubtedly bisporangiate, as microspores were isolated from the sporophylls near the tip, and megaspores are present throughout the basal part. It is apparently slightly smaller than *Mazocarpon oedipternum,* and the sporophylls are alternately arranged in seemingly definite verticils, about ten per whorl. This verticillate arrangement is apparently the feature which determined its classification under *Sigillariostrobus.* No peduncle is present, and Miss LeClercq describes the cone in her diagnosis (op. cit. p. 168) as sessile. From the specimen as it is illustrated one cannot be sure that the cone was actually sessile, but if it was it cannot be placed in *Sigillariostrobus* but must be placed in *Lepidostrobus* instead (see discussion of peduncle on p. 26). With the exception of its strict verticillate phyllotaxy it conforms better with *Lepidostrobus,* and this character is by no means diagnostic of *Sigillariostrobus.*

Miss LeClercq (op. cit. p. 165, footnote) states that the ornamentation of the megaspores of *S. sphenophylloides* is distinctive and matches that of Zerndt's type 14. Now the type 14 megaspores of Zerndt are quite variable and surely comprise quite a group of species (cf. Zerndt 1940, p. 148). Nearly all would be classed in the aphanozonate section of *Triletes,* (Schopf, 1938). However, it does not seem that the megaspores described by Miss LeClercq actually have their closest alliance with the type 14 megaspores of Zerndt or with the *Aphanozonati.* The megaspore she illustrates in proximal view on her plate II, figure 2, seems to have a typically folded lageniculate apex with vestibule (cf. Schopf, 1938, p. 27). Although a few of the spines on the macerated spore on her plate IV, figure 10, are short and stout, this is probably due to chemical attack since others appear to be much longer, more slender, and slightly sinuous, or curved. Miss LeClercq indicates that the apiculae are all the same size (op. cit., p. 165) and also mentions that some of the spines bifurcate, although she does not illustrate this feature. The megaspore coats are imperfectly macerated but fairly translucent, judging from her photographs taken by transmitted light. All these characters (with the exception of the bifurcate spines) are represented at least partially in *Triletes (Lagenicula) kidstoni,* in part, as described and illustrated by Zerndt (1934, p. 26-27; cf. pl. 28, figs. 2 and 3; and 1937, pl. 16,

figs. 1 and 8).[10] This also suggests an alliance with *Lepidostrobus* rather than with *Sigillariostrobus*, since lageniculate megaspores have their known relationship with the former group.

Some of the microspores reported from *S. sphenophylloides* are exceptionally large (85 μ). Others, supposed to be immature, are about 35 μ in diameter. The former exceed those of *Mazocarpon* in size but the latter are small enough to match those of *Lepidostrobus*. Conclusive information on the morphology of the microspores might be of considerable value in identifying the genus, but apparently Miss LeClercq's material did not macerate very well and the characters are not clearly defined on any of the microspores shown.

The sporophylls of *S. sphenophylloides* were caducous as in several other species of *Sigillariostrobus* and in *Mazocarpon shorense*. However this is of little or no diagnostic value because caducous isolated sporophylls of *Ortholepidostrobus* (Arber 1922, p. 173) are at least as abundant as those of *Sigillariostrobus, Mazocarpon*, or other genera.

For these various reasons it may be concluded that *Sigillariostrobus sphenophylloides* LeClercq is not conclusively identified as to genus and hence should not be relied upon for evidence relating to cones of *Sigillariostrobus*. The cone probably belongs to *Lepidostrobus* instead, and the occurrence of bisexuality in it may not be as unique a feature as was supposed. It is from beds of lower Pennsylvanian age, and whether it is particularly related to verticillate *Lepidostrobus* of the Lower Carboniferous is not clear.

No other reports of bisexual cones of *Sigillariostrobus* are known to the author. It seems that there is little trustworthy evidence that bisexual cones occurred in the sigillarian alliance, particularly during Pennsylvanian time. There is likewise no evidence of bisexual cones occurring in *Mazocarpon*. Miss Benson assumed that cones of *Mazocarpon shorense* were bisexual, but this was supported by no direct evidence. So far as the evidence goes, again there is no apparent disparity between *Mazocarpon* and *Sigillariostrobus* in regard to unisexuality of the cones produced. Records of microsporangiate cones of *Sigillariostrobus* are so largely inferential that this apparent agreement cannot be given undue weight at present. Nevertheless, it seems most likely that unisexual microsporangiate cones of *Sigillariostrobus* will be proved if an adequate study is undertaken.

The cones of some Lower Carboniferous (Mississippian) sigillarians may have been typically bisexual because the unisexual cones of *Mazocarpon* must be taken as quite highly specialized and as derived from a more primitive condition. At some point in the sigillarian ancestry the cones must have been bisexual. Only a few species of modern *Selaginella* (cf. Mitchell, 1910) attain similar specialization among the living lycopods. Nevertheless, unisexual cones are quite in keeping with other features of Pennsylvanian sigillarians which have been mentioned, such as the pedunculate mode of fructification, specialization of the gametophyte, characteristics of the megasporangium, etc., all of which exceed the modern forms so far as relative structural modification is concerned.

One of the strongest sources of evidence indicating the alliance of *Sigillariostrobus* and *Mazocarpon* is in the megaspores themselves. These are sufficiently large and abundant in *Sigillariostrobus* cones to have been noted by several observers. The megaspores in general are those which the author has previously concluded must be classified together in the aphanozonate section of *Triletes*. This decision originally was based on a comparative study of spore morphology. It was recognized that the presence or absence of apiculae was a character of importance only for specific discrimination, and megaspores reported from cones of *Sigillariostrobus* strongly tend to confirm this view. In most descriptions of *Sigillariostrobus* species the spore characteristics are not fully reported, and there is some ques-

[10] Megaspores which are at least very closely related to *Triletes (Lagenicula) kidstoni* Zerndt have been isolated from Caseyville coals of the Illinois basin and also from thin Mississippian coals in the upper part of the Chester series.

tion as to the reliability of specific differences indicated by small-scale drawings. Consequently these illustrations are of little value in systematic study of the spores. On the other hand, by working with both the isolated spores and the cones containing megaspores, more satisfactory conclusions have been reached. All compression - preserved cones which are recognized as containing aphanozonate megaspores have been identified by various earlier authors as *Sigillariostrobus*—not as the more common *Lepidostrobus*. This does not mean that all cones identified as *Sigillariostrobus* contained aphanozonate megaspores. The case of *S. sphenophylloides* has been discussed, and in several *Sigillariostrobus* species spores are not reported.

It was not until the present study was under way that it was realized that the megaspores of *Mazocarpon* resembled characteristic members of the aphanozonate section of *Triletes* (Schopf, 1938). The megaspores of *M. oedipternum* can easily be dissolved from the coal-ball matrix by dilute hydrochloric acid, and such spores display surface characteristics somewhat better than the spores obtained from nitric acid maceration residues of coal. Arcuate ridges of these spores dissolved from coal-balls appear somewhat fainter than is usual for *Triletes reinschi*. Spores similar to these from *M. oedipternum* but obtained by ordinary maceration of coal would probably be difficult or impossible to distinguish from *T. reinschi*. There is no question as to their close relationship with that species although uncertainty may exist as to their actual identity. In a previous paper (Schopf 1938, p. 25) the probable relationship of *T. reinschi* to several species as identified on the basis of cone characteristics was pointed out. For example, spores isolated from *Sigillariostrobus czarnockii* would probably also be referred to *T. reinschi* because the megaspore coats in both instances possess similar features.

Apiculate members of *Aphanozonati (Triletes brevispiculus)* are only moderately abundant in certain benches of the Herrin (No. 6) coal bed in Illinois. Coal maceration studies continued since 1938 indicate their rarity or absence from the greater part of the overlying McLeansboro. In lower Pennsylvanian "Pottsville" beds, apiculate *Aphanozonati* are found more abundantly, and the spines, which are the chief means of differentiating species, are more prominent. *Triletes mamillarius* Bartlett is of this group and also many of those spores which Zerndt (1934, pp. 17-18) has classified as type 14. These are all from beds of some degree of stratigraphic coincidence, possibly falling in the lower and middle Westphalian,[11] (cf. text fig. 1 for approximate equivalence of stratigraphic terms). The horizon from which *Mazocarpon shorense* was derived belongs in lower Westphalian A. The megaspores from this cone are also prominently apiculate. From the illustrations given, one cannot tell much about the type of ornamentation of *M. shorense* megaspores because all are from sections. One may hope that a full description of the English *Mazocarpon* spores will be provided, as a good description is unavailable at present. In view of the agreement in the forms obtained in sections with those in sections from cones of *M. oedipternum*, there can be no doubt that the *M. shorense* megaspores fall in the aphanozonate section of the genus *Triletes* along with megaspores of the type known from *Sigillariostrobus ciliatus, S. rhombibracteatus, S. czarnockii, S. tieghemi* (cf. illustrations in Kidston, 1897; Zeiller, 1884, etc.) and the others which have been discussed. This agreement, in the opinion of the writer, is one of the strongest reasons for considering *Mazocarpon* and *Sigillariostrobus* to be closely related. The number of megaspores in sporangia in the two groups is not necessarily discordant. They are not very numerous in sporangia of any species of *Sigillariostrobus* although the numbers in individual sporangia cannot be established with the same accuracy as in petrified material of *Mazocarpon*.

It is evident from the preceding discussion that biological criteria distin-

[11]Zerndt, 1940, p. 143, indicates that his type 14 spores extend through the Westphalian D, but are not found in the Stephanian.

guishing *Sigillariostrobus* from *Mazocarpon* are notably absent. In large part, therefore, the distinction between the groups is probably artificial in that the chief distinction is not based on heritable characteristics but on differences in preservation which prohibit a comparison of critical features. The demonstrable presence of intrasporangial tissue in *Mazocarpon* is the only outstanding criterion not known from *Sigillariostrobus*. Bochenski (1936) mentions that the megaspores of *S. czarnockii* occasionally bear a faint reticulate imprint. This may be due to a "ramental" remnant of intrasporangial tissue as in the case of spores of *M. oedipternum*, (p. 17) and if so it is the first record of such tissue from compression fossils. If exact correlative relationship is ever proved between these two genera, abundant evidence of this sort must be sought. In the meantime the basic information relating to the sigillarians seems to be more clearly indicated if the present grouping is maintained. The likelihood is that these genera could be merged for specimens of Pennsylvanian age without violating any phylogenetic concepts. In the earlier history of the sigillarian alliance, difficulties in interpretation are bound to arise that will hinge on definition of the genera. It will probably simplify the problems if nomenclature is applied strictly, even though this results in the same biological group being generally represented under several generic terms recognized as partially synonymous.

SPECIFIC RELATIONSHIPS

There are no available records of *Sigillariostrobus* in any beds adjacent to the Calhoun horizon in Illinois. Cones of *Mazocarpon oedipternum* should be easily recognized in impressions or compressions by the unique character of lamina and dorsal heel of sporophylls, and later investigation may disclose them. *Lepidophyllum brevifolium* Lesquereux (1858) and the allied form, *L. minutifolium* Lesquereux (1884), appear to have similar very short laminae, but other information is lacking and a close relationship is dubious. Both of Lesquereux's species are recorded from appreciably lower Pennsylvanian horizons.

The *Sigillariostrobus* cone, designated as *Lycopodites lacoei* by Lesquereux (1884, p. 780), is from Oliphant No. 1 bed in the anthracite field of Pennsylvania, of about middle Conemaugh age. It seems to be nearer to the age of the Calhoun horizon than other forms of *Sigillariostrobus*. The sporophylls of *"Lycopodites" lacoei* are longer than those of *Mazocarpon oedipternum*, and more numerous sporophylls seem to be present in each whorl. The spores are unknown, but in Lesquereux' drawing (op. cit., pl. CVII, fig. 1) the sporangia appear relatively tumid and somewhat similar to those of *Mazocarpon*. However close the generic affinity between *Mazocarpon* and *Sigillariostrobus* may be, there seems no close specific relationship between *M. oedipternum* and species of either *Mazocarpon* or *Sigillariostrobus*, at least so far as the general size and form of the sporophyll allows us to judge.

Mazocarpon shorense, on the other hand, appears to be more closely related to certain species of *Sigillariostrobus* than to either the older species, *Mazocarpon pettycurense*, or to *M. oedipternum*. In length the *M. shorense* sporophyll laminae seem to be about the same as in *Sigillariostrobus ciliatus* Kidston, *S. czarnockii* Bochenski, and *S. gothani* Bode. The latter two species are distinct from *M. shorense* in that they both appear to have levigate megaspores, and also they are both geologically younger than *M. shorense*. The megaspores and other details of *Sigillariostrobus ciliatus* are in closer agreement with *M. shorense* and they are probably rather closely related. There is, of course, no adequate basis for considering them specifically identical. *Sigillariostrobus czarnockii* and *S. gothani* appear closely related to each other although the information available for *S. gothani* is

not entirely satisfactory.[12] The cone peduncle is not demonstrable and the distal tip of the cone is missing. However, judging from their imprint, the spores are clearly of the aphanozonate type and may also be represented among isolated spores of *Triletes reinschi*. The sporophylls are either verticillate or in a very low spiral. There is no character which conflicts with its identification as *Sigillariostrobus*, although important characters are not represented.

RELATION OF PALEOZOIC LYCOPOD GROUPS

Pennsylvanian sigillarians are a much more specialized group than many of the contemporaneous lepidodendrids. These two main groups of arboreous lycopods surely had a common phyletic source, and there has been a tendency to confuse the two groups, particularly in discussions of their fructifications. Consequently some discussion of certain lepidodendrid genera is pertinent here in order to bring out further the reasons for considering them as distinct lineages through Pennsylvanian and somewhat later time.

One of the chief lepidodendrid groups bearing on this discussion is *Lepidostrobus*, a genus identified by characteristics of its cones and to a large extent approximately correlative with *Lepidodendron*. Except for the large size attained by some species, *Lepidostrobus* seems to have been the least specialized of the arboreous Paleozoic lycopods throughout the Carboniferous. *Mesostrobus* Watson (1909) appears in the lower Westphalian (Mountain 4-ft. mine, Clough foot, Dulesgate = Great Coalball horizon [?]) of England and may be regarded as a segregate from the main line of *Lepidostrobus*. No great specialization is manifest and it is unlikely that specimens of *Mesostrobus* can be distinguished from *Lepidostrobus*, when preserved as coalified compressions.

There also are some highly specialized forms frequently placed with the lepidodendrids that are distinguished as the Lepidocarpaceae. Whether these specialized forms actually belong in the lepidodendrid groups (typical representatives of which are *Lepidodendron* and *Lepidostrobus*) or should be considered a separate group on a par with the lepidodendrids and sigillarians, need not be given special consideration now; it has been discussed elsewhere (Schopf, 1941) and the author is inclined to think segregation will prove desirable. There is little reason to doubt that the lepidocarps (typically represented by *Lepidocarpon*, *Illiniocarpon*, and possibly (?) *Lepidophloios*) are more closely related to the lepidodendrids than they are to the sigillarians or any other major lycopod group.[13] However, the specialization observed in *Lepidocarpon* has been confused with the distinct type of specialization encountered in *Mazocarpon*. Consequently it is worth while to point out these distinctions in somewhat greater detail.

The Free-Sporing Character of Mazocarpon

One source of confusion arises apparently from a misunderstanding of the true morphologic nature of the *Mazocarpon* sporangium. Miss Benson and others since 1918 have frequently termed the *Mazocarpon* female fructifications "seed-like". This terminology appears unacceptable according to the writer's interpretation of *Mazocarpon oedipternum*. The prolonged association of sporophytic tissue with *Mazocarpon* mega-

[12] Bode (1928) indicates that only three megaspores were borne "naked" on each sporophyll of *S. gothani*. The difficulty in distinguishing contents of individual sporangia in compression material makes the uniform presence of three megaspores doubtful. It is perhaps significant, however, that they were at least no more numerous than in species of *Mazocarpon*. Bode's suggestion that the spores "lie naked on the bract" and that the sporangium is lacking, is too highly anomalous to be accepted at its face value. He cites *Flemingites* Carruthers (1865) as a parallel example, but it was shown long ago by Binney (1871) and others that Carruthers' genus was based on a misconception.

[13] The grouping of the lepidocarps with *Miadesmia* under the name *"Lepidospermae"* (Hirmer 1927) and assignment to ordinal rank by Zimmermann (1930) seems unwarranted. *Miadesmia* has only the remotest possible relationship with any of the arboreous forms.

spores is the result of lack of an effective mechanism for bursting open the sporangia, such as is present, for example, in *Selaginella* (Mitchell, 1910). Despite this, the essential free-sporing adaptations are not materially altered in *Mazocarpon*. The thickness of the megaspore coats indicates that the nutritional bond between sporophyte and gametophyte was not any greater than in other free-sporing plants. The occurrence of intrasporangial tissue has no essential bearing on the question since it has no effective connection with the mature growth of the gametophytes. The writer considers that the intrasporangial tissue served no essential protective or nutritive function after formation of the spore coat. Any effect the persistent intrasporangial tissue may have had on spore distribution is that which would result in any free-sporing plants with poorly dehiscent sporangia. There seems to be no valid reason why these megaspores or sporangia should be termed "seed-like". Such a designation merely confuses the useful distinction between free-sporing and seed-bearing plants.

Mazocarpon and Lepidocarpon

On the other hand, the lepidocarps have every claim to recognition as true seeds because they possess all the physical and physiological attributes of the seed habit. The lepidocarp megasporangium is indehiscent. The seed megaspore is greatly enlarged, the megaspore membrane is modified for facile interchange of food materials and has lost its original essential function as a protective membrane just as much as in any of the Paleozoic gymnospermic seeds. The sporophytic structure is specialized to form a protective integument, and the sporophyll lamina is probably effective as a dispersal mechanism. The distinctive feature of *Mazocarpon*, viz. the extraordinary development of intrasporangial tissue (function unknown) is not characteristic of *Lepidocarpon* or of *Lepidostrobus*. The most distinctive feature of *Lepidocarpon*, the elaboration of an effective integument, is not suggested by either *Mazocarpon* or *Lepidostrobus*. Although it has often been overlooked, Scott pointed out that the integument of *Lepidocarpon* appears as a *new organ* and cannot be interpreted as a mere upfolding of the lateral wings of the pedicel. That this was a correct interpretation is borne out by the study of *Illiniocarpon* in which the integument is still further elaborated and is entirely distinct from the sporophyll lamina.

Miss Benson further confused this issue when she suggested (Benson, 1920) that *Cantheliophorus* Bassler (1919) was identical with *Sigillariostrobus* and compared favorably with *Mazocarpon*. Recent studies (Schopf, 1940, 1941) indicate that *Cantheliophorus* Bassler shows the seed megaspores and integuments which characterize the genus *Lepidocarpon* and, despite the differences in preservation, should be identified with it. The relationship of *Cantheliophorus* and *Sigillariostrobus* is entirely indirect.

The relationship between seed-bearing *Lepidocarpon* and essentially free-sporing *Mazocarpon* can not be regarded as direct. The two are more reasonably interpreted as divergent specialized reproductive types among the Carboniferous lycopods. Miss Benson's statement (1918, p. 582) that "*Mazocarpon* is exactly intermediate between *Lepidostrobus* and *Lepidocarpon*" is without basis either as an analogy or homology since entirely diverse specializations distinguish the two groups. Both were coexistent over a long period of geological time. *Lepidocarpon wildianum* was described from the Calciferous Sandstone of Burntisland by Scott in 1901, and Walton (1936) has recently mentioned the occurrence of *Lepidocarpon* in beds of the Lower Carboniferous Cementstone group from the Isle of Arran. It thus at least equals and may even antedate the existence of both *Mazocarpon* and *Sigillariostrobus*.

Mazocarpon and Spencerites

The resemblance of *Mazocarpon oedipternum* and plants classified as *Spencerites* is interesting chiefly because of the obscurity of the affinities of *Spencerites*. However, despite these similarities, there is no proof of a direct relationship be-

tween the two groups, and until we have real evidence that *Spencerites* is either heterosporous or homosporous, surmises are not warranted. Scott, at one time at least, entertained the possibility that *Spencerites insignis* might have some sigillarian connection, although no proof of this or any other alliance has been forthcoming.[14]

The notable features of *Spencerites* which may be compared with *Mazocarpon* are: (1) The cones in both genera are pedunculate with the peduncle of *Spencerites* bearing "irregular bracts" somewhat as in *M. oedipternum;* (2) the cone axis sometimes has a "pith" and sometimes is solid in individual species of both genera; (3) sporophylls of *Spencerites* have not yet shown any trace of a ligule; in *M. oedipternum* the presence of a ligule is hard to demonstrate although it has been found in a few instances. Although theoretical interpretation would hold that the ligule of *M. oedipternum* is probably always present this is not proved, and the reported absence of a ligule in *Spencerites* may also be because it is ephemeral and hard to find;[15] (4) the sporophylls of *Spencerites* may vary in arrangement from spiral to verticillate in the same manner as has been described for *M. oedipternum* (cf. Berridge, 1905, p. 275). Such phyllotactic variability is often present among modern lycopods, consequently neither this similarity nor, in fact, any of the others just mentioned, can be taken as necessarily suggestive of phyletic alliance.

CONCLUSION

Mazocarpon oedipternum clearly indicates from its geological position that the *Mazocarpon* type of sigillarian fructification existed at least throughout most of Pennsylvanian time. During this period it seems unlikely that any sigillarian fructifications deviated very much from the *Mazocarpon* type, but specimens preserved as compressions (*Sigillariostrobus*) probably are not entirely corgeneric although they may coincide for a considerable part of their respective geologic time ranges. Evidence from several sources shows the overlapping relationship of these generic groups, and similar types of evidence link them definitely with *Sigillaria.* However, as frequently is the case for fossil plant material, conclusive evidence is lacking for species. Thus, although the assignment of these genera to a "sigillarian alliance" may hardly be questioned in its broader aspects, the species nomenclature should remain essentially the same; if anything the species should be more strictly defined.

The sigillarian alliance thus outlined probably has little relationship in common with the lepidodendrids of the period despite similarities in many anatomical details. *Lepidocarpon* shows no close phyletic relationship to *Mazocarpon* but instead represents a parallel line of specialization tracing back historically as far as *Mazocarpon* itself. *Lepidostrobus* is a plant group, of lepidodendrid alliance, which lacks the sporangial elaboration shown in different ways by *Lepidocarpon* and *Mazocarpon. Lepidostrobus* is present in the American uppermost Devonian, according to Read and Campbell (1939), and thus is the most ancient representative of the groups mentioned. Probably the two specialized lines originated from this unspecialized (but geologically persistent) lepidostrobid stock early in Mississippian time, although it may have been still earlier. Considerable interest attaches to definition of the specialized groups in the Mississippian in view of their probable phyletic deri-

[14]The discussion of the relationship of *Spencerites* and other forms given by Watson in 1909 does not accord with historical facts as known at present. For example, *Lepidostrobus kentuckyensis* Scott and Jeffrey is from the uppermost Devonian, according to recent studies by C. B. Read (Read and Campbell, 1939). Evidently therefore, *Lepidostrobus* cannot be regarded as a derivative of the much younger forms of *Spencerites* and *Mesostrobus* from beds equivalent to the lower Pennsylvanian in age. If there is any direct phyletic connection the sequence must be reversed from that which Watson suggested. *Lepidostrobus* shows no characters indicative of a highly advanced type but represents chiefly enlargement of a primitive heterosporous type of cone. The writer considers it less advanced than the relatively primitive but modern genus *Selaginella.*

[15]Actually very few specimens of *Spencerites* cones have been studied.

vation in this time interval.

During Pennsylvanian time these lycopod alliances apparently were distinct. It appears from the present study that Pennsylvanian fossils of lepidodendrid alliance need not be confused with sigillarian types in phyletic consideration. If a precise evolutionary sequence of sigillarian fossils (or any others for that matter) can be established in detail these fossils will become much more useful as stratigraphic indices, and further investigation along this line is contemplated.

Aphanozonate megaspores seem definitely linked with the sigillarians. In a general way it seems that apiculate species of *Aphanozonati* represent characteristic sigillarians in the Lower Pennsylvanian rocks, whereas levigate *Aphanozonati* are more abundant in the Upper Pennsylvanian. Detailed studies of these species based on isolated spores and spores associated with sigillarian cones should help in further indicating the sigillarian evolutionary sequence as well as in serving directly stratigraphic purposes. As these spores are obtainable from coal, they also will aid in evaluating the importance of sigillarians in coal formation. Thus, the greater abundance of the aphanozonate species *Triletes reinschi* and *Triletes brevispiculus* in the Herrin (No. 6) coal (Schopf, 1938, pp. 27, 29) in the coal bench immediately overlying the blue-band clay parting is one of the factors to be considered in explaining the origin of this type of coal. Furthermore the importance of the sigillarians as plants capable of establishing themselves on what must have been a dense clay substratum (the blue-band) must be recognized. These aphanozonate spores are by no means alone in this portion of the coal bed but, in marked contrast to some of the other species present, they are definitely more abundant there.

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DESCRIPTION OF PLATES

All specimens illustrated are in the collections of the Illinois State Geological Survey at Urbana. Relative magnification of the figures is accurately given by linear scales adjacent to each or as noted in description of the figures.

PLATE 1.—Mazocarpon oedipternum forma megalophorum

Fig. 1. Part of a nearly radial section of cone: From C. B. 136 (20).

2. Part of a nearly radial section of cone including median section of normal sporophyll (N Sp). From C. B. 136 (20).

3. Tangential section of cone suggesting a low spiral arrangement of sporophylls: From C. B. 136 (9).

4. Tangential section of cone transecting sporangia toward the distal end and showing lateral keels of sporangia (SpK) inclined downward: From C. B. 136 (3).


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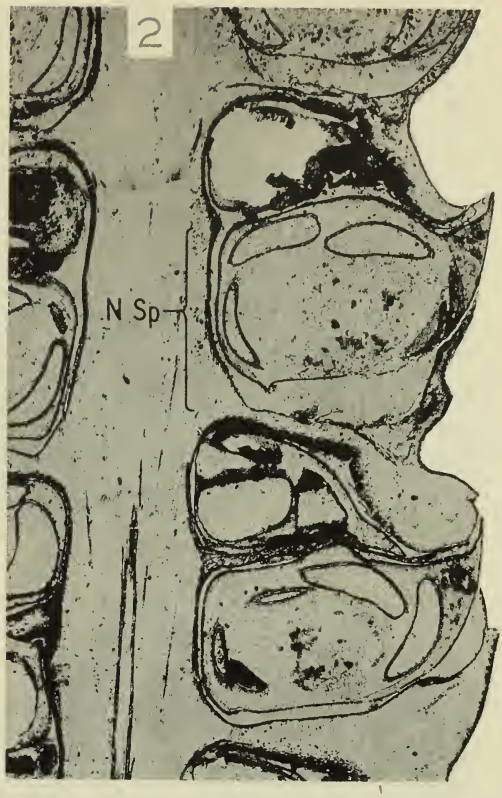
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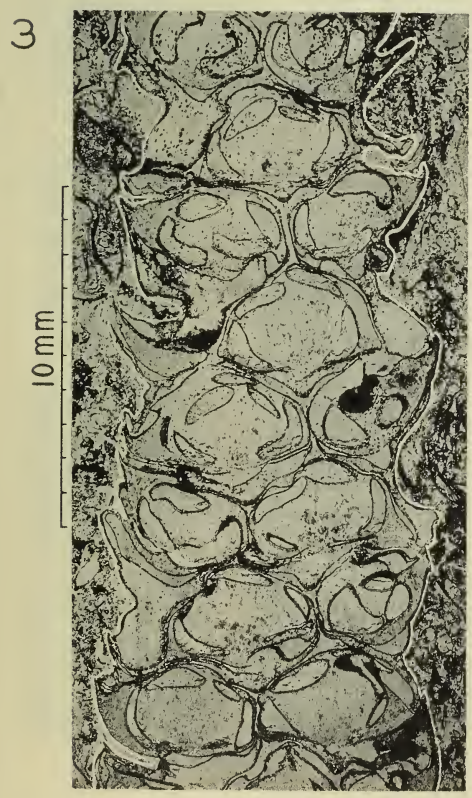
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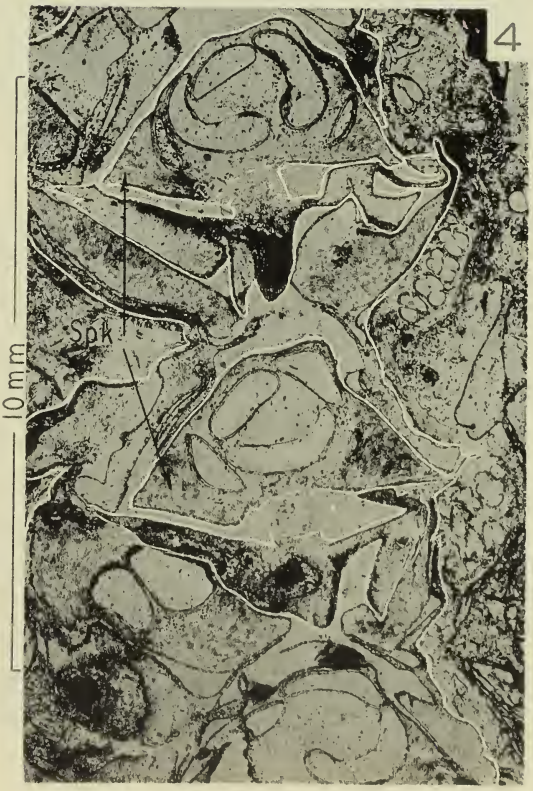
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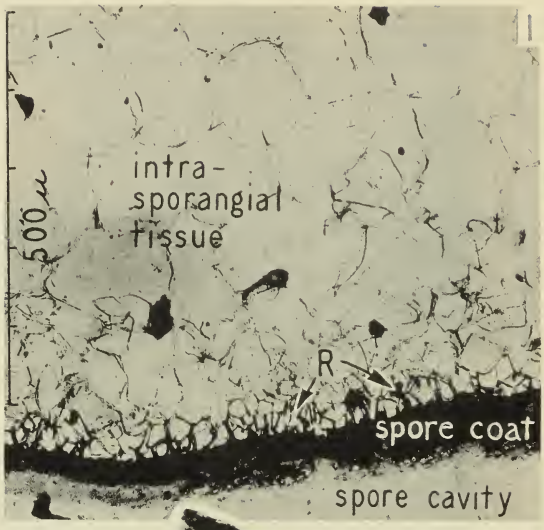
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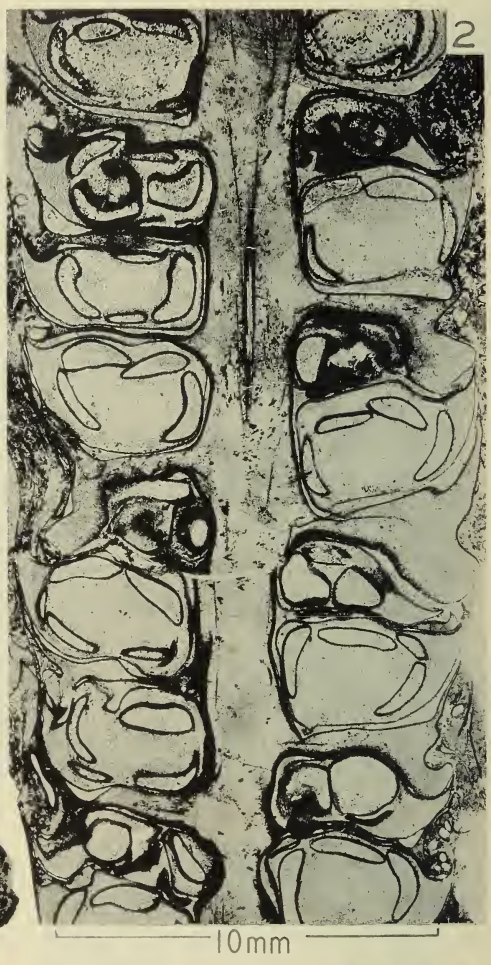
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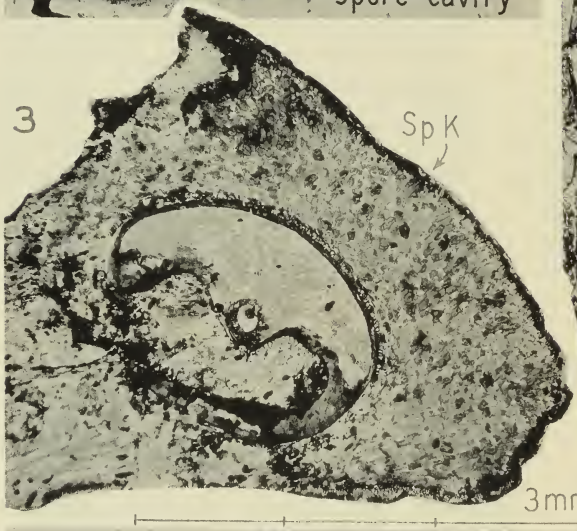
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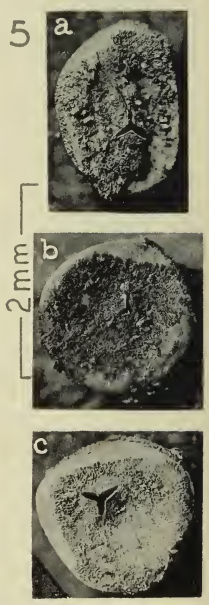
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PLATE 2.—Mazocarpon oedipternum forma Megalophorum

FIG. 1. Photograph showing connection between the cellular "ramentum" (R) on concave proximal surface of megaspore and the intrasporangial tissue: From C. B. 136 (18).

2. Nearly radial thin-section through cone. Compare with text fig. 5b: From C. B. 136 (24).

3. Section across distal end of more or less fragmented sporangium, transecting the apical prominence of the most distal megaspore. A greater thickness of the sporangial keel (SpK) is cut in this plane. The tissue of the keel is well shown: From C. B. 136 (34).

4. Transverse section of sporophyll (tangential to cone axis) taken near the proximal end of the sporangium. Thin areas (T) in the prismatic outer layer of the sporangium may be seen. Central tissue is well shown; cells are much larger than those in the sporangial keel (compare with fig. 3): From C. B. 136 (20).

5a, b, c. Megaspores of *Mazocarpon oedipternum* [corresponding to *Triletes reinschi* (pars.)] isolated by solution of calcite coal-ball matrix. In some areas "ramentum" has scaled off. Spore photos by E. A. Platt.

PLATE 3.—Female Gametophytes of Mazocarpon oedipternum

Fig. 1. Small isolated globule of tissue observed in chamber of gametophyte at apex of spore; illustrated at lower magnification on plate 2, figure 3: From C. B. 136 (34).

2. Small isolated globule of tissue (8-12 cells) in chamber of gametophytic tissue at apex of megaspore: From 130 C2 (5).

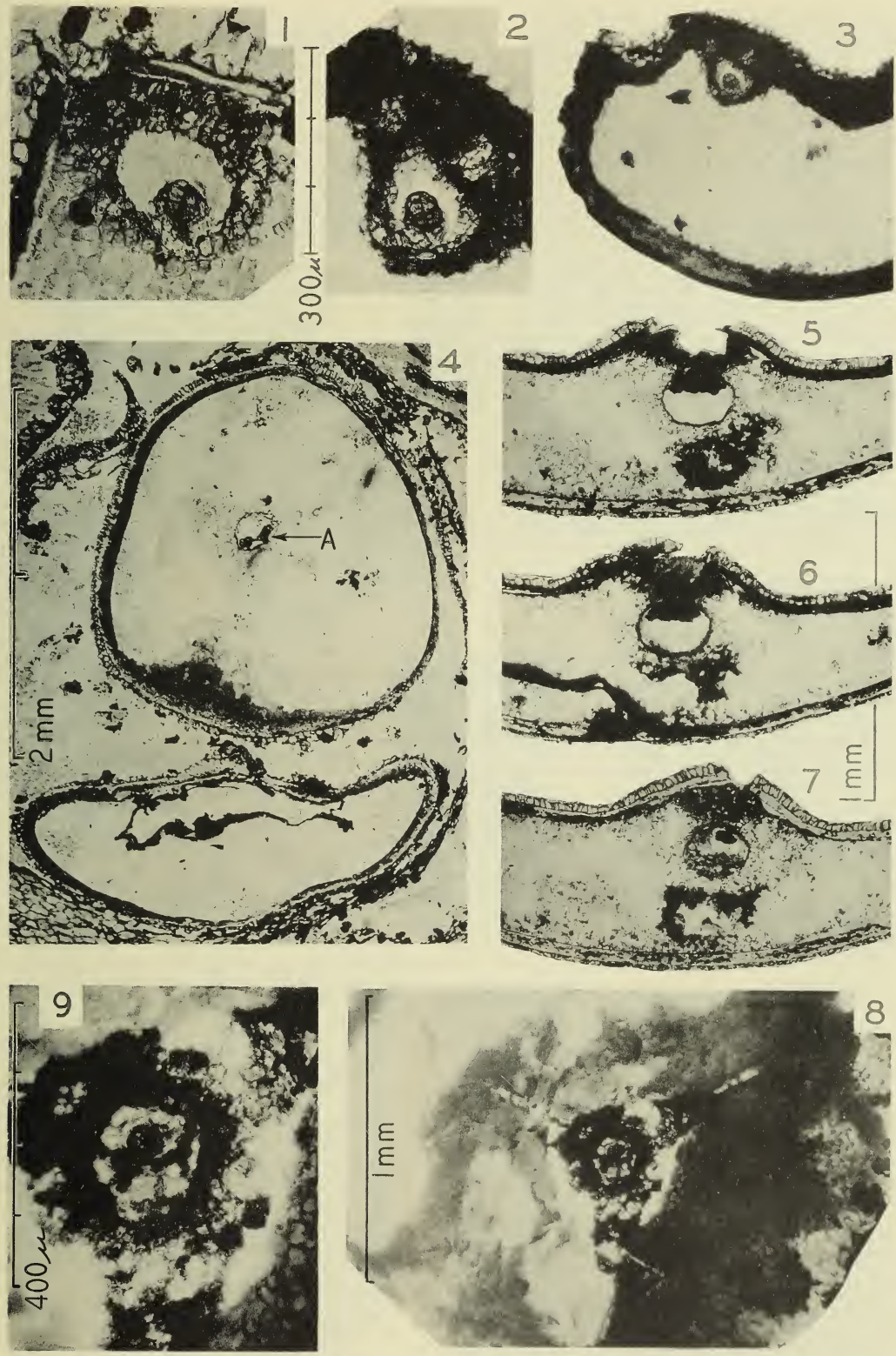
3. Gametophytic chamber (fig. 2) shown in relation to the rest of the spore at lower magnification (same as for figs. 5, 6, and 7). The chamber is at the spore apex; except in this area the megaspore cavity is filled by crystalline calcite devoid of tissue. Spore coat appears thicker than normal because it is cut obliquely: From 130 C2 (5).

4. Sections of two megaspores oriented at right angles to one another. An archegonium, also shown on plate 4, figure 5 (A), surrounded by very delicate gametophytic tissue, is seen (cut transversely) in the spore at the top. The spore below shows shrunken endosporal membrane: From C. B. 116 A 3b, (T6).

5, 6, 7. Three successive longitudinal sections of a megaspore with delicate gametophytic tissue and apical archegonium. Figure 5 is median and shows neck of archegonium protruding slightly into apical vestibule. Figures 6 and 7 are at more tangential levels respectively. A dark humic mass occupies the neck and top of the venter: Sections at same magnification, from C. B. 116 A3 (T3) and 116 A3b (T4) and (T5) respectively.

8. Transverse section of apex of megaspore showing trilete rays and section through top of archegonium: From C. B. 130 B.

9. Archegonium (fig. 8) at higher magnification. A red humic globule occurs in the center of archegonium which is filled with more dispersed flocculent humic material.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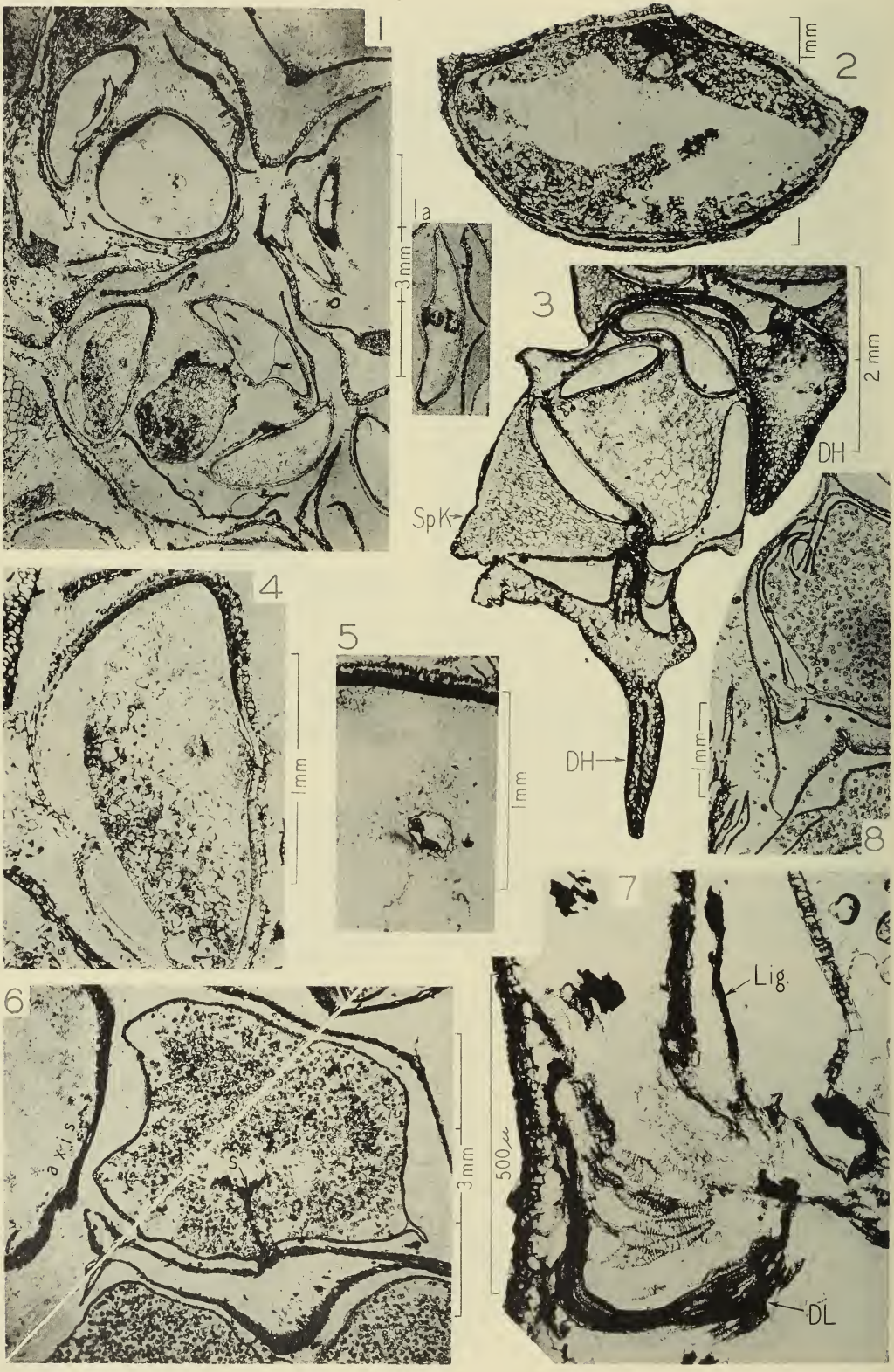
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PLATE 4.—Mazocarpon oedipternum

Fig. 1. Section of portions of somewhat fragmented sporophylls cut tangential to cone axis and containing megaspores with gametophytes.

1a. Megaspore with gametophyte and archegonium from same section as fig. 1. Compare with plate 3, figs. 5, 6, 7: From C. B. 116 A3b (T5).

2. Megaspore with fusainized gametophytic tissue. Archegonium at apex cut tangentially: From C. B. 116 A3b (T3).

3. Transverse section of sporophylls (tangential to cone axis) proximal to great expansion of dorsal heel, (DH). Sporangium on left appears to have only one lateral sporangial keel (SpK), the other having been eliminated due to crowding: From C. B. 136.

4. Megaspore with partially fusainized gametophyte shrunken away from distal spore wall. A small tangential slice of the archegonial venter is shown: From C. B. 116 A3b (T5).

5. Archegonium, same as shown near center, fig. 1, at higher magnification. Delicate gametophytic tissue and some cells of venter can be seen: From C. B. 116 A3b (T6).

6. Proximal section of microsporangium adjacent to cone axis. Section from two planes as in plate 5, figs. 1 and 3; sporangial attachment and collapsed T-shaped vestige of subarchesporial pad (s) is shown: From C. B. 124 E (T34).

7. Median longitudinal section passing through dorsal loop (DL) of sporophyll trace in *M. oedipternum* f. *microphorum*. Scalariform "transfusion" type tracheids occur inside the loop. A shrunken remnant of the ligule (Lig.) is shown above the downturn of the loop: From C. B. 124 E (32).

8. Distal end of same sporophyll from which fig. 7 was taken, showing relation of sporophyll trace to sporangium, etc. Compare with text fig. 3b.

PLATE 5.—Mazocarpon oedipternum

Fig. 1. Forma *microphorum*; slightly oblique longitudinal (near-radial) and transverse sections at the tip of a cone, obtained simultaneously on a single peel. Ruled white line indicates juncture of the two planes of section: From C. B. 124 E (T38).

2. Forma *megalophorum*; transverse section for comparison with similar sections of f. *microphorum* in figs. 1 and 3: From C. B. 136.

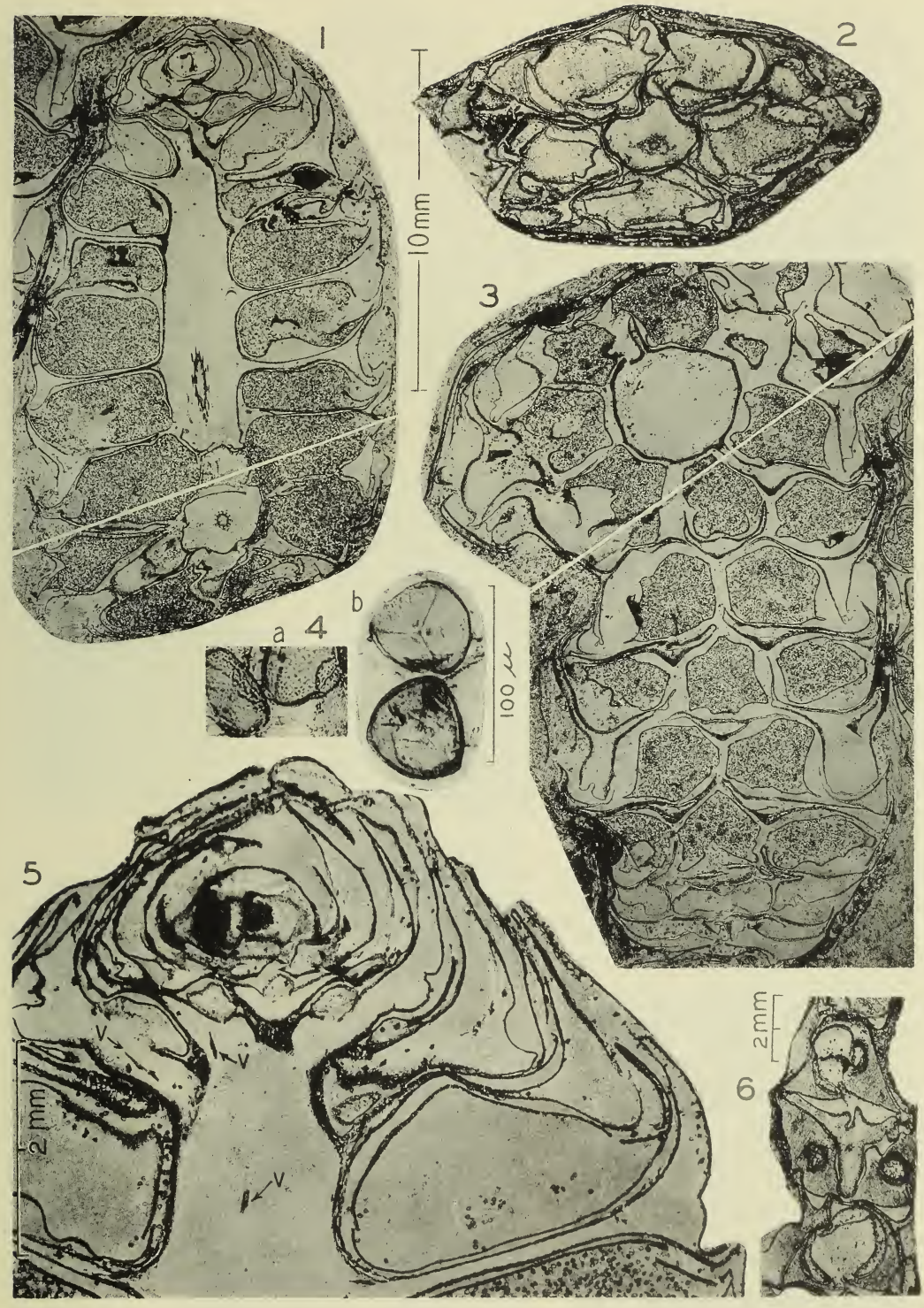
3. Forma *microphorum*; section taken in the same manner as that shown in fig. 1 but through the basal part of a different cone. Longitudinal section is tangential. Sterile sporophylls are shown at the cone base. Stele has disintegrated and is absent in the oblique transverse part of the section: From C. B. 124 E (T38).

4a. Microspores showing papillate surpace of exospore.

4b. Exospore more or less torn off, exposing the endospore which is shown carrying the trilete sutures. A thickened darker spot is shown at the tip of each pyramic segment of the endospore. Spore photos by E. A. Platt.

5. Section at higher magnification taken slightly tangential to microsporangiate cone apex. Vascular traces (v) extend into undeveloped sporophylls at cone tip. Strict verticillate arrangement is evident: From C. B. 124 E (T32).

6. Forma *megalophorum*; tangential section of cone shown in fig. 2 adjacent to the plane shown on a slant at the left of that figure. Sporophylls are apparently in verticills: From C. B. 136.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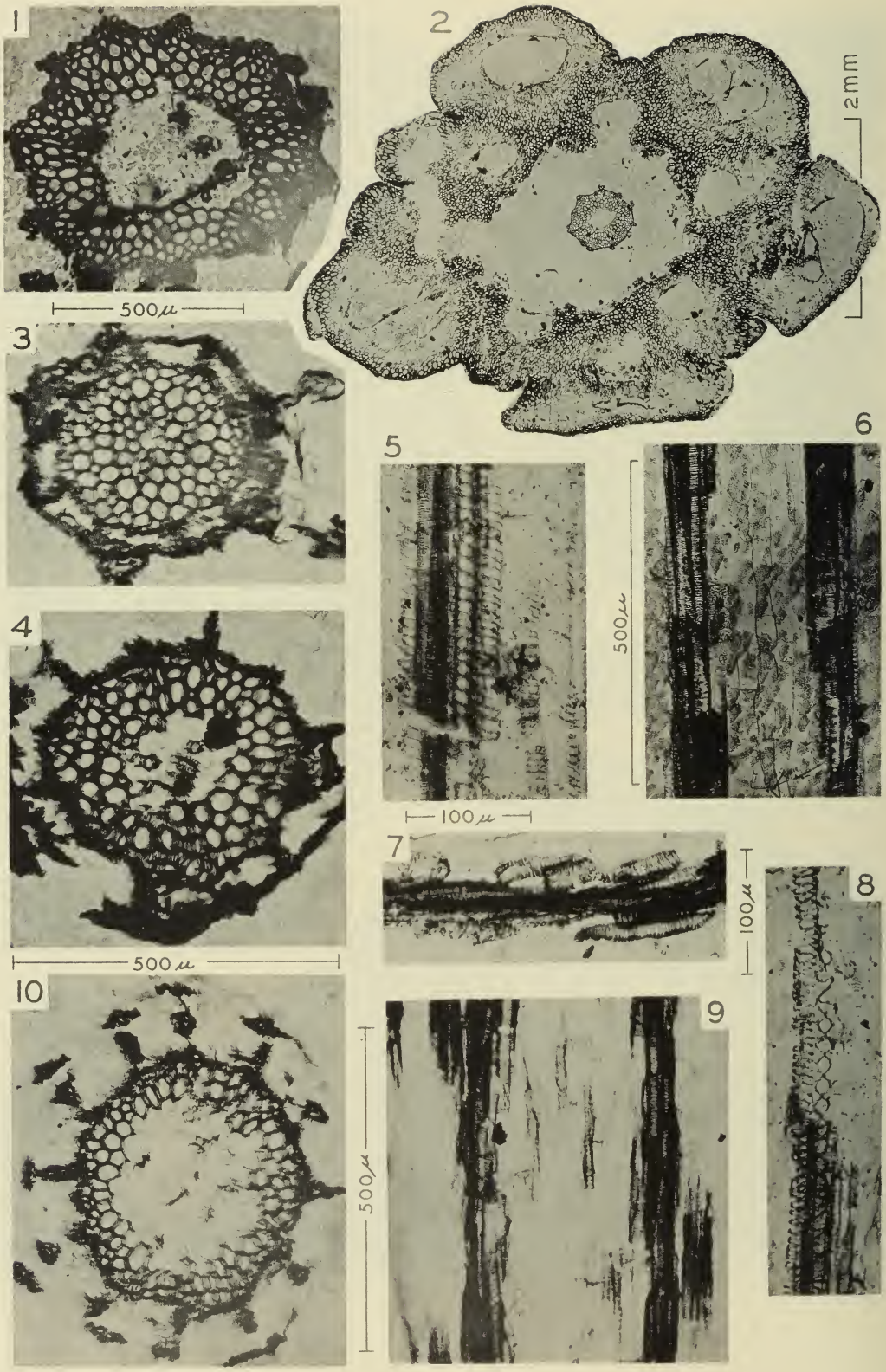
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PLATE 6.—Penduncle and Vascular Structure of
MAZOCARPON OEDIPTERNUM

FIG. 1. Transverse section of peduncular stele with isolated tracheid groups in medullary area: From C. B. 136 A.

2. Transverse section of peduncle showing bract bases (with large parichnoidal cavities) in spiral arrangement. Inner cortex not preserved: From C. B. 195 D (T1).

3. Transverse section of stele in cone axis essentially lacking prosenchymatous medulla. Stele is slightly larger than those shown in figs. 4 and 10 (compare magnification scales): From C. B. 139.

4. Transverse section of stele in cone axis showing relatively large thickness of metaxylem and small medullary area with scattered central tracheids: From C. B. 130 B.

5. Extreme tangential section of stele showing spiral elements in sporophyll trace and on the outside of the adjacent stele. A few scalariform elements also are entering the trace: From C. B. 136 (18).

6. Longitudinal section of stele in megasporangiate cone axis showing prosenchymatous medullary cells, scalariform metaxylem, and annular and spiral protoxylem tracheids: From C. B. 136 (21).

7. Horizontal portion of trace from sporophyll pedicel consisting chiefly of scalariform tracheids: From C. B. 136 (18).

8. Sporophyll trace ascending from the stele in cone axis showing spiral, annular, and scalariform tracheids: From C. B. 136 (18).

9. Longitudinal section of stele also shown in fig. 10 (cf. also plate 5, fig. 1) showing annular medullary tracheids, scalariform metaxylem tracheids and outgoing sporophyll traces: From C. B. 124 E (T34).

10. Transverse section of stele in cone axis (cf. plate 5, fig. 1) showing verticillate arrangement of outgoing sporophyll traces. Isolated medullary tracheids are present: From C. B. 124 E (T34).